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BIBLIOTECA  
CENTRO DE ECOLOGIA

#### DARWIN'S THEORY

When Charles Darwin boarded the Beagle in late 1831 for his famous voyage he took with him volume one of Charles Lyell's *Principles of Geology*, which had been published in 1830. Darwin's teacher John Henslow had recommended the book to him with the admonition not to accept Lyell's views. Like most geologists of the time, Henslow was a catastrophist. He believed the geological history of the earth was progressive, that is, showed significant changes, and was characterized by successive cataclysms with periods of little change in between. Adam Sedgwick, president of the Geological Society in 1831 and Darwin's other teacher of geology, was also a catastrophist. With two catastrophists as his teachers Darwin naturally adopted their general view of geological change. But he did not think catastrophism provided a complete explanation of geological change. He said to a friend, "it strikes me that all our knowledge about the structure of the earth is very much like what an old hen would know of a hundred-acre field, in a corner of which she is scratching."<sup>1</sup>

In the *Principles* Lyell challenged, as James Hutton had before him, the prevalent geological theories of catastrophism and progressionism. Lyell believed the geological history of the earth could be explained by the same agents that were operating at present, given enough time. This was the principle of uniformitarianism. He went further and rejected progressionism. He held that geological forces had made only minor changes in the earth's surface, and not even a cumulation of geological events could cause a major change.

The impact of volume one of Lyell's *Principles* upon Dar-

1. Francis Darwin, ed., *The Life and Letters of Charles Darwin*, 3 vols. (London: John Murray, 1887), 2:348.

win's thought was quick and deep. Only twenty days after the start of the Beagle's voyage, the first ten of which he was miserably seasick, Darwin landed at St. Iago in the Cape Verde Islands and was there convinced, as he later said, of "the infinite superiority of Lyell's views over those advocated in any other work known to me."<sup>2</sup> This was a remarkable transformation in such a short period of time.

St. Iago was a perfect place to convince Darwin of Lyell's belief in gradual geological change. At first glance, the island might have appeared to be a perfect example of catastrophism. It had extinct volcanoes and a twenty-foot-thick layer of white limestone, which had been deposited beneath the water, now elevated sixty feet above sea level. But Darwin was looking for evidence of Lyell's theory, and he found it right under the catastrophists' volcano: the horizontal layers of rock all bent down into the water in the neighborhood of the volcano, indicating gradual subsidence of the crater.

Lyell's ideas thus gained an auspicious start in Darwin's mind. He said later that St. Iago "showed me clearly the wonderful superiority of Lyell's manner of treating geology, compared with that of any other author, whose works I had with me or ever afterwards read."<sup>3</sup> Observing geological patterns during the rest of the Beagle's voyage and reading volumes two and three of the *Principles* thoroughly convinced Darwin that Lyell's thesis of gradual change was a true explanation of geological events.

At no time, however, was Darwin convinced of Lyell's objection to progressive change. He observed too many examples of the great rearrangements caused by the cumulative effects of smaller changes. For example, at Port Desire, on the east coast of South America, he saw beds containing shells from currently existing species that had been raised to a height of 330 feet above sea level. From his reading of Lyell and his observations on the voyage of the Beagle, Darwin returned

2. Charles Darwin, *Autobiography*, ed. Nora Barlow (London: Collins, 1958), p. 101.

3. Ibid., p. 77.

to England in 1836 confirmed in the belief that geological change was gradual but progressive.

Ever since his visit to St. Iago at the start of the voyage, Darwin had wanted to write a book on geology. In the ten years after his return he produced three: *The Structure and Distribution of Coral Reefs* (1842), *Geological Observations on the Volcanic Islands* (1844), and *Geological Observations on South America* (1846). All three books embodied the idea of gradual geological change—an idea evidently deep-seated in Darwin's mind.

Darwin considered what he had learned from Lyell in geology to be applicable to biological problems. Speaking of his initial attempt to shed light on the modification of species he later wrote:

After my return to England it appeared to me that by following the example of Lyell in geology, and by collecting all facts which bore in any way on the variation of animals and plants under domestication and nature, some light might perhaps be thrown on the whole subject.<sup>4</sup>

T. H. Huxley, in his obituary notice for Darwin, commented on the success with which Darwin used Lyell's ideas:

It is hardly too much to say that Darwin's greatest work is the outcome of the unflinching application to Biology of the leading ideas and the method applied in the "Principles" to geology.<sup>5</sup>

Darwin did not adopt Lyell's ideas about the modification of species, since Lyell's conception of uniformitarianism precluded the possibility of progressive changes in species. What Darwin did apply to the problem of species modification was the same thing he learned from Lyell to apply to geology, namely, the idea of gradual change.

From the beginning of his work on the modification of species Darwin was strongly inclined toward the view of gradual change. When he became convinced that species did

4. Ibid., p. 119.

5. Thomas H. Huxley, *Darwiniana* (New York: D. Appleton, 1896), p. 268.

in fact change, he supposed "that species gradually became modified."<sup>6</sup> The mechanism of species change for which he searched would reflect this attitude.

In July 1837, Darwin began the first of three notebooks on the transmutation of species. By October 1838, he had read Malthus and come to a tentative formulation of the idea of natural selection, the mechanism of species change. Darwin's early vision of natural selection was a simple and clear generalization:

If variation be admitted to occur occasionally in some wild animals, and how can we doubt it, when we see [all] thousands (of) organisms, for whatever use taken by man, do vary. If we admit such variations tend to be hereditary, and how can we doubt it when we (remember) resemblances of feature and character,—disease and monstrosities inherited and endless races produced (1200 cabbages). If we admit selection is steadily at work, and who will doubt it, when he considers amount of food on an average fixed and reproductive powers act in geometrical ratio. If we admit that external conditions vary, as all geology proclaims, they have done and are now doing,—then, if no law of nature be opposed, there must occasionally be formed races, [slightly] differing from the parent races.<sup>7</sup>

In short, variation exists and is heritable; more organisms are born than can possibly survive on the available supply of food; therefore, those organisms with variations best suited to the environment survive more often and new races are occasionally formed. Thus stated, Huxley's comment seems apt: "How extremely stupid not to have thought of that!"<sup>8</sup> Yet the idea of natural selection involved difficulties which Darwin was never able to overcome fully, which invited the criticism of his friends as well as his opponents, and which were not satisfactorily solved until the rise of population

6. Darwin, *Autobiography*, p. 119.

7. Charles Darwin and Alfred Russel Wallace, *Evolution by Natural Selection* (including "Sketch of 1842," "Essay of 1844," and "Papers of 1858"), ed. Francis Darwin (Cambridge: University Press, 1958), "Sketch of 1842," p. 57. Words in [ ] were erased by Darwin; words in ( ) are editor's insertions.

8. Leonard Huxley, *Life and Letters of Thomas Henry Huxley*, 2 vols. (New York: D. Appleton, 1900), 1:183.

genetics. There were two basic interconnected problems: the character and origin of the variation upon which natural selection acts, and Darwin's assumption of blending inheritance.

Darwin believed that variation was a basic property of species of organisms. In 1842, when he wrote the first sketch of his theory of species modification, he stated at the beginning that

. . . simple generation, especially under new conditions [when no crossing] causes infinite variation . . . There seems to be no part . . . of body, internal or external, or mind or habits, or instincts which does not vary in some small degree and [often] some to a great amount.<sup>9</sup>

Domestication usually subjected organisms to changed conditions and thus produced more variation than was normally found under natural conditions. But a change of conditions in nature would have the similar effect of causing more variation. New variation was produced each generation.

The variations, as Darwin and most breeders recognized, were of two types. There were sports, large discontinuous variations, relatively rare but sometimes used to good advantage by breeders. The Ancon sheep with short stubby legs was a case of sporting which Darwin mentions on several occasions. Besides sports, there were the less obvious but more pervasive and plentiful minor variations which occurred in every character of the organism. Every species exhibited these minor variations and Darwin believed they were increased when the species was subject to changed conditions. He termed these minor variations "mere variability" or, more often, "individual differences."

Darwin thought both kinds of variation were often inherited. In the very first paragraph of the "Sketch of 1842," speaking of the variations produced by changed conditions, he stated "most of these slight variations tend to become hereditary."<sup>10</sup> Thus variation was a fundamental property of

9. "Sketch of 1842," pp. 41-42.

10. Ibid., p. 41.

species. Under changed conditions variation was bursting out of the population and was mostly heritable.

In the face of so much new variation with each generation, a species could scarcely retain constant characters over a period of generations except by some mechanism which enforced uniformity. To Darwin's mind, blending inheritance supplied this mechanism. Blending of characters may be observed in most sexually reproducing populations and the prevalent opinion in Darwin's time was that the hereditary material itself blended. He adopted that view.<sup>11</sup>

Blending inheritance fit nicely with Darwin's ideas about variation since it kept a species uniform in the face of burgeoning variation. In the "Sketch of 1842," Darwin states that free crossing is a "great agent in producing uniformity in any breed."<sup>12</sup> And in the first edition of the *Origin* he says, "Intercrossing plays a very important part in nature in keeping individuals of the same species, or of the same variety, true and uniform in character."<sup>13</sup> Darwin believed that blending inheritance worked upon both sports and individual differences. He recognized, however, that some sports were prepotent to some degree. They would appear more fully formed in the offspring than predicted by the blending theory. Other sports Darwin recognized as reversions to ancestral characters. Sports of these kinds were dissipated more slowly by blending inheritance but were dissipated nevertheless.

Thus for Darwin sexual reproduction was an agent of uniformity not diversity. He believed more variation occurred in sexually reproducing organisms than in those which reproduced asexually. Otherwise, asexually reproducing organisms, with no blending inheritance to assist, would not be able to exhibit the uniformity all naturalists observed. Darwin thought sexual reproduction was actually more widespread than did his contemporaries because of the vigor it unleashed

11. For a detailed account see Peter Vorzimmer, "Charles Darwin and Blending Inheritance," *Isis* 54 (1963): 371-90.

12. "Sketch of 1842," p. 42.

13. Charles Darwin, *The Origin of Species: A Variorum Text*, ed. Morse Peckham (Philadelphia: University of Pennsylvania Press, 1959), p. 195 (hereafter cited as Peckham).

in the offspring under certain conditions. It followed that variation, fodder for natural selection, was also more widespread but kept in check by interbreeding.

The problem of selection in Darwin's mind was how it operated in the face of blending inheritance. If unchecked, blending would demolish the variation upon which selection acted: "If in any country or district all animals of one species be allowed freely to cross, any small tendency in them to vary will be constantly counteracted."<sup>14</sup> "In man's methodical selection, a breeder selects for some definite object, and free intercrossing will wholly stop his work."<sup>15</sup> For selection to be effective, intercrossing had to be suppressed.

In the case of artificial selection the solution was obvious: the person selecting would isolate from the rest of the population those organisms which exhibited the characters he wanted to perpetuate. Blending inheritance would have no chance to dissipate the new characters. Artificial selection might therefore be quite rapid.

Natural selection, however, presented more difficult problems and Darwin did not reach satisfactory solutions for them until many years later. At first he thought the process of natural selection was similar to that of artificial selection. A beneficial variant might be isolated with a small number of his species. Blending inheritance would then dilute the beneficial character of the variant, but if the isolated group were small enough, then "there would be a chance of the new and more serviceable form being nevertheless in some slight degree preserved."<sup>16</sup> The single beneficial variant Darwin had in mind here was what he had termed a "sport." Yet the discontinuous variant could only lead to a minor change in the isolated segment of the population; and this process fit perfectly with Darwin's belief that evolution occurred gradually. Even when he believed that the primary source of variation was discontinuous, he believed that the evolutionary change of the species was gradual and continuous.

14. "Sketch of 1842," pp. 42-43.

15. Peckham, p. 193.

16. Darwin, "Essay of 1844," p. 198.

The idea of natural selection suggested by Darwin in the "Essay of 1844" soon became untenable for him. Sports were rare, and often one of a kind. For natural selection to proceed, more variation was necessary. Moreover, the geographical isolation postulated as necessary by Darwin occurred rarely. For selection to proceed, the rare variant would have to be isolated with a few members of his species by an unusual occurrence. The combination of rarities did not seem convincing to Darwin, who was looking for the all-pervasive mechanism of species change under nature.

By 1856, when he was writing on a projected exposition of his theory of natural selection, Darwin had found some answers. He was now convinced that sports were too rare to be the primary source of variation; in addition, sports were often infertile and easily swamped by blending inheritance in any but the smallest populations. So he turned instead to the other sort of variation, small but plentiful in every species—individual differences. It is crucial to remember that from the time he wrote the first sentence of the "Sketch of 1842," quoted above, until his death, Darwin believed that many of the individual differences were inherited.

Each generation produced individual differences in each character of a species. The variations tended to occur in every direction, giving natural selection a convenient, if small, handle. For instance, in a species of foxes, some would be born with longer claws than most of the population and some with shorter. If the long claws conferred an advantage, then those foxes would survive better and leave more offspring. Gradually more of the foxes would have longer claws and an evolutionary change would have occurred in the species. Isolation was no longer necessary for evolution in a species; enough variation was produced each generation for selection to operate effectively.

This way of looking at natural selection, that is, as operating upon individual differences, fit perfectly with Darwin's idea of geological change derived from Lyell. With this mechanism evolution was necessarily a gradual and con-

tinuous process; yet great changes could be effected given enough time. It was basically this theory of species change which Darwin presented in the first edition of the *Origin of Species* in 1859.

He did not believe this theory was final. Because of blending inheritance, the theory required that much new heritable variation be produced each generation; otherwise blending would destroy the variation upon which natural selection acted. But the mechanism which produced individual differences was not known to Darwin, as he admitted in the first *Origin*:

I have hitherto sometimes spoken as if the variations—so common and multiform in organic beings under domestication, and in a lesser degree in those in a state of nature—had been due to chance. This, of course, is a wholly incorrect expression, but it serves to acknowledge plainly our ignorance of the cause of each particular variation.<sup>17</sup>

The critics were quick to seize Darwin's profession of ignorance on the production of variation as a loophole into which other possibilities could be inserted. Many claimed that the production of variations was directed and that the variations, rather than natural selection, determined the direction of evolution.

In 1868, Darwin finally produced his "Provisional Hypothesis of Pangenesis,"<sup>18</sup> an attempt to supply a theory of heredity that would account for the production of huge numbers of heritable individual differences. Basically, the theory stated that each part of an organism throws off "free and minute atoms of their contents, that is gemmules."<sup>19</sup> The gemmules multiply and aggregate in the reproductive apparatus, from

17. Peckham, p. 275.

18. Charles Darwin, *The Variation of Plants and Animals under Domestication*, 2 vols. (New York: Orange Judd, 1868), vol. 2, chap. 27. For an account of the development of Darwin's thought on pangenesis, see Gerald L. Geison, "Darwin and Heredity: the Evolution of His Hypothesis of Pangenesis," *Journal of the History of Medicine* 24 (1969): 375-411.

19. Darwin, *Variation*, 2:481.

which they are passed on to the following generations. The theory was designed so that the "direct and indirect" influences of the "conditions of life" might become embodied in the hereditary constitution of the organism. If an organism were affected by the environment, the affected parts would throw off changed gemmules which would be inherited, perhaps causing the offspring to vary in a similar fashion. With his theory of pangenesis to account for the production of individual differences, Darwin's theory of the origin of species was complete.

#### THE REACTION

Contrary to popular belief, the reaction among most biologists to Darwin's idea of the evolution of species was not strongly adverse, especially after the initial impact of the *Origin*.<sup>20</sup> The idea of evolution was not new, having appeared prominently in the works of Buffon, Erasmus Darwin, Lamarck, and many others. A popular book in England since its publication in 1844 was Robert Chambers's *Vestiges of the Natural History of Creation*,<sup>21</sup> a treatise on organic evolution. The huge amount of evidence for evolution that Darwin had collected was convincingly presented in the *Origin*. Most biologists and many others soon came to believe in it.

Darwin's idea of natural selection, however, did arouse a very strong reaction. The random production of variation, with the relentless elimination of the less fit variants, ran entirely against the prevalent view of "design" in nature. The Reverend Dr. Hodge of Princeton University, echoing the feelings of many, stated that "to ignore design as manifested in God's creation is to dethrone God."<sup>22</sup> That the beauty and harmony of living creatures was the result of chance rather than design was abhorrent to most minds.

20. See Alvar Ellegård, *Darwin and the General Reader: The Reception of Darwin's Theory of Evolution in the British Periodical Press, 1859-1872*, Gothenburg Studies in English, vol. 8 (Göteborg: Elanders Bohtryckeri Aktiebolag, 1958).

21. The *Vestiges* went through eleven editions, about twenty-four thousand copies.

22. Quoted by Andrew Dickson White, *A History of the Warfare of Science and Religion*, 2 vols. (New York: D. Appleton, 1930), 1:79.

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Design in nature was not inconsistent with evolution since the unfolding of new organic forms could be seen as resulting from a higher order, from a master plan. But Darwin's idea of natural selection denied this possibility. Thus Darwin was in the curious position of having convinced most scholars that evolution had occurred but not by the means he envisioned. Most of the serious attacks upon Darwinism centered upon the idea of natural selection.

Many of these attacks were initiated by thinkers who found natural selection abhorrent for nonscientific reasons. The production of variation was a favorite target, and Darwin admitted his weakness in this area. But the attacks were not accompanied by convincing substitutes for the mechanism of evolution. Most of the alternate proposals suggested a non-material force which directed the production of variation and, consequently, the direction of evolution. These theories did not find widespread acceptance.

Out of the assault upon natural selection emerged ideas which were instrumental in the rise of population genetics. Curiously enough, this criticism came from two of Darwin's staunchest supporters and admirers, Thomas H. Huxley and Francis Galton. Darwin firmly believed that individual differences were the significant source of variation, that natural selection was the motive agent, and that the movement of evolution was both gradual and continuous. Huxley and Galton challenged Darwin's emphasis upon individual differences. They suggested instead that selection primarily utilized discontinuous variations, or sports, and in consequence that evolution might proceed rapidly and by discontinuous leaps. The criticism and suggestions offered by Huxley and Galton are important, for the division between those who believed in the natural selection of individual differences and continuous evolution and those who believed in a mutation theory and discontinuous evolution was the common thread in the development of population genetics.

#### THOMAS H. HUXLEY AND "NATURA NON FACIT SALTUM"

Thomas H. Huxley was perhaps the most articulate and vigorous of the early champions of Darwin's ideas. He once

said, "I am Darwin's bull-dog," and many of Darwin's critics suffered under his onslaughts. Yet he was among the very first to criticize Darwin's treatment of variation and continuity in evolution. Immediately upon reading the first edition of the *Origin*, Huxley wrote Darwin that "you have loaded yourself with an unnecessary difficulty in adopting *Natura non facit saltum* so unreservedly."<sup>23</sup> The unnecessary difficulty was that the gaps between existing species and in the geological record could not easily be explained if natural selection operated only upon individual differences, because intermediate forms would be expected. Such gaps were to be expected, however, if the raw material for natural selection were discontinuous variations, or what Huxley termed "saltations."

Five months prior to the publication of the *Origin*, Lyell told Huxley that the transmutation theory could not account for the distinct gaps between species, living and fossil. Huxley's reply in a letter of 25 June 1859 states clearly the position he held until the end of his life.

The fixity and definite limitation of species, genera, and larger groups appear to me to be perfectly consistent with the theory of transmutation. In other words, I think *transmutation* may take place without transition.

Suppose that external conditions acting on species *A* give rise to a new species, *B*; the difference between the two species is a certain definable amount which may be called *A-B*. Now I know of no evidence to show that the interval between the two species must necessarily be bridged over by a series of forms; each of which shall occupy, as it occurs, a fraction of the distance between *A* and *B*. On the contrary, in the history of the Ancon sheep, and of the six-fingered Maltese family, given by Réaumur, it appears that the new form appeared at once in full perfection.

I may illustrate what I mean by a chemical example. In an organic compound, having a precise and definite composition, you may effect all sorts of transmutations by substituting an atom of one element for an atom of another element. You may in this way produce a vast series of modifications—but each modification is definite in its composition, and there are no transitional or intermediate steps between one definite com-

23. T. H. Huxley to C. Darwin, 23 November 1850, in L. Huxley, *Life and Letters of Thomas Henry Huxley*, 1:189.

pound and another. I have a sort of notion that similar laws of definite combination rule over the modifications of organic bodies, and that in passing from species to species "*Natura facit saltum*."<sup>24</sup>

That natural selection acted upon saltations, instead of individual differences, was for Huxley precisely what harmonized the theory of natural selection and the evidence of geology. Indeed, he believed that the transmutation of species was the natural extension of Lyell's uniformitarianism.

Huxley believed, as did Darwin, that selection played a decisive role in evolution. Speaking of his own two examples, Ancon sheep and hexadactyl humans, Huxley states that in one "a race was produced, because, for several generations, care was taken to select both parents of the breeding stock from animals exhibiting a tendency to vary in the same direction; while, in the other, no race was evolved, because no such selection was exercised."<sup>25</sup> Darwin would never have admitted that natural selection could act so quickly, in "several" generations.

Huxley believed saltations to be more stable and less susceptible to the effects of blending inheritance than did Darwin: "If a variation which approaches the nature of a monstrosity can survive thus forcibly to reproduce itself, is it not wonderful that less aberrant modifications should tend to be preserved even more strongly."<sup>26</sup> These "less aberrant modifications" Darwin would never have considered individual differences, since Ancon sheep are given as an example. Instead the variations referred to by Huxley are more like the "discontinuous variations" later described by William Bateson and called "sports" by Darwin. Huxley's idea of evolution appears to have more in common with de Vries's and Bateson's than with Darwin's.

24. T. H. Huxley to Sir Charles Lyell, 25 June 1859, *ibid.*, pp. 185-86. Considering recent knowledge of the mutations in DNA, the hereditary material, Huxley's last paragraph seems to be a remarkable anticipation of modern genetical thought.

25. T. H. Huxley, "Darwin on the Origin of Species," *Westminster Review*, n.s., 17 (1860): 550.

26. *Ibid.*, p. 549.

## FRANCIS GALTON, REGRESSION, AND DISCONTINUOUS EVOLUTION

Francis Galton greatly admired his cousin Charles Darwin, and certainly Darwin influenced Galton's scientific researches. Four years after Darwin's death Galton had this to say:

Few can have been more profoundly influenced than I was by his publications. They enlarged the horizon of my ideas. I drew from them the breath of a fuller scientific life, and I owe more of my later scientific impulses to the influences of Charles Darwin than I can easily express. I rarely approached his genial presence without an almost overwhelming sense of devotion and reverence, and I valued his encouragement and approbation more perhaps, than that of the whole world besides.<sup>27</sup>

But Galton's brilliant and acute mind scarcely allowed him to agree with Darwin when his own researches conflicted with his cousin's ideas. Galton disagreed most with Darwin on the issues of hereditary variation and continuity in evolution. Huxley probably influenced Galton on these issues, but no direct evidence for this is available.

In 1869, Galton published his book *Hereditary Genius*, a preliminary attempt to analyze the inheritance of genius. He was certain that genius was a hereditary trait and that a genius had a distinctly superior intellect compared to other humans. The spectrum of human intelligence was not uniform, and each type of intelligence seemed to be stable. In the concluding chapter, in a passage which was often quoted by his contemporaries, Galton explained what he meant by stability of types and how that was connected with evolution:

I will now explain what I presume ought to be understood, when we speak of the stability of types, and what is the nature of the changes through which one type yields to another . . . It is shown by Mr. Darwin, in his great theory of *The Origin of Species*, that all forms of organic life are in some sense convertible into one another, for all have, according to his views, sprung from common ancestry, and therefore A and B having both descended from C, the lines of descent might be remounted from A to C, and redescended from C to B.

27. From speech of Francis Galton delivered at the Royal Society, 1886. Recorded in Karl Pearson, *The Life, Letters, and Labours of Francis Galton*, 3 vols. (Cambridge: Cambridge University Press, 1914-30), 2:201 (hereafter cited as *Galton*).

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Yet the changes are not insensible gradations; there are many, but not an infinite number of intermediate links; how is the law of continuity to be satisfied by a series of changes in jerks? The mechanical conception would be that of a rough stone, having, in consequence of its roughness, a vast number of natural facets, on any one of which it might rest in "stable" equilibrium. That is to say, when pushed it would somewhat yield, when pushed much harder it would again yield, but in a less degree; in either case, on pressure being withdrawn it would fall back into its first position. But, if by a powerful effort the stone is compelled to overpass the limits of the facet on which it has hitherto found rest, it will tumble over into a new position of stability, whence just the same proceedings must be gone through as before, before it can be dislodged and rolled another step onwards. The various positions of stable equilibrium may be looked upon as so many typical attitudes of the stone, the type being more durable as the limits of its stability are wide. We also see clearly that there is no violation of the law of continuity in the movements of the stone, though it can repose in certain widely separated positions.<sup>28</sup>

Galton at this time already believed that evolution proceeded by discontinuous leaps, a belief he later expressed in more detail.

When writing *Hereditary Genius* Galton based his comments about heredity upon Darwin's hypothesis of pangenesis. Galton's theory of stability of types did not, however, seem to fit with pangenesis, which Darwin had developed primarily to account for the production of hereditary individual differences. Galton therefore decided to test pangenesis experimentally. Darwin had stated that the gemmules "circulate freely throughout the system" and that "the gemmules in each organism must be thoroughly diffused; nor does this seem improbable considering their minuteness, and the steady circulation of fluids throughout the body."<sup>29</sup> Assuming Darwin meant that the gemmules circulated in the blood stream of higher animals, Galton embarked, with Darwin's encouragement, upon an attempt to transfuse the blood of different varieties of rabbits. If the offspring of the

28. Francis Galton, *Hereditary Genius* (reprint of 1892 edition, New York: Meridian Books, 1962), pp. 421-22.

29. Darwin, *Variation*, 2:448, 454.

transfused rabbits were mongrelized, Darwin's theory would be proved.

The first experiments were negative. The offspring of the transfused rabbits were in no way affected. After improving the technique of transfusion, Galton attempted another series of experiments on rabbits, all negative. On 30 March 1871, Galton read a paper before the Royal Society in which he stated that "the doctrine of Pangenesis, pure and simple, as I have interpreted it, is incorrect."<sup>30</sup>

Darwin reacted by writing a letter to *Nature* published on 27 April. Galton's interesting experiments, he said, proved little. Nowhere had he stated that the gemmules must travel in the blood stream, so Galton's proof that the gemmules could not be in the blood did not destroy the theory of pangenesis. Darwin admitted that when Galton was performing the experiments he "did not sufficiently reflect on the subject, and saw not the difficulty of believing in the presence of gemmules in the blood."<sup>31</sup>

Galton replied with a letter to *Nature* published on 4 May. After showing that Darwin's ambiguous language in his statement of pangenesis might easily be interpreted to mean that the gemmules would be in the blood stream, Galton concluded:

I do not much complain of having been sent on a false quest by ambiguous language, for I know how difficult it is to put thoughts into accurate speech, and, again, how words have conveyed false impressions on the simplest matters from the earliest times. Nay, even in the idyllic scene which Mr. Darwin has sketched of the first invention of language, awkward blunders must of necessity have occurred. I refer to the passage in which he supposes some unusually wise ape-like animal to have first thought of imitating the growl of a beast of prey so as to indicate to his fellow-monkeys the nature of expected danger. For my part, I feel as if I had just

30. Francis Galton, "Experiments in Pangenesis by Breeding from Rabbits of a Pure Variety into Whose Circulation Blood Taken from Other Varieties Had Been Infused," *Proceedings of the Royal Society* 19 (1871): 404.

31. Darwin to *Nature*, 27 April 1871, reprinted in Pearson, *Galton*, 2:163.

been assisting at such a scene. As if, having heard my trusted leader utter a cry, not particularly well articulated, but to my ears more like that of a hyena than any other animal, and seeing none of my companions stir a step, I had, like a loyal member of the flock, dashed down a path of which I had happily caught sight, into the plain below, followed by the approving nods and kindly grunts of my wise and most respected chief. And now I feel, after returning from my hard expedition, full of information that the suspected danger was a mistake, for there was no sign of a hyena anywhere in the neighborhood. I am given to understand for the first time that my leader's cry had no reference to a hyena in the plain, but to a leopard somewhere up in the trees; his throat had been a little out of order—that was all. Well, my labour has not been in vain; it is something to have established the fact that there are no hyenas in the plain, and I think I see my way to a good position to look out for leopards among the branches of the trees. In the meantime, Vive Pangenesis!<sup>32</sup>

Galton's dissatisfaction with Darwin's theory of heredity is visible beneath his humor. Pangenesis was not the "leopard among the branches" that Galton now sought.

Although he considered Darwin his "wise and most respected chief," Galton's ideas on heredity and evolution were to be sufficiently different from those of Darwin that thirty-five years after the pangenesis experiments some of the most outspoken anti-Darwinists claimed to trace their intellectual heritage to Galton. Curiously, some of the most respected Darwinists of that time also claimed Galton as their inspiration. The reasons for this incongruous situation are discussed in chapter 2.

Although Galton knew he had not definitely disproved Darwin's theory of pangenesis, he began to search for a theory of heredity which would harmonize with his belief in the discontinuity in variation. By 1875 his theory was taking definite shape. The hereditary qualities, instead of being imbedded in gemmules which were formed in all parts of an organism, were concentrated in the reproductive organs. The germ plasm, or "stirp," was continuously inherited from generation to generation with little alteration. One corollary was

32. Galton to *Nature*, 4 May 1871, *ibid.*, p. 165.

that hereditary variations were caused by alterations of the "stirp" and were quite distinct. Another corollary was that acquired characters were unlikely to affect the germ plasm, as would happen under the hypothesis of pangenesis.

With his own theory of heredity in hand, Galton again examined the problem of continuity in evolution. There can be no doubt that he advocated the idea of evolution by discontinuous leaps. In 1894, after discussing some instances of sports described by Darwin in *Variation of Plants and Animals under Domestication*, Galton states that "many, if not most breeds, have had their origin in sports." He goes on to say:

Notwithstanding a multitude of striking cases of the above description collected by Darwin, the most marked impression left on his mind by the sum of all his investigations was the paramount effect of the accumulation of a succession of petty differences through the influence of natural selection. This is certainly the prevalent idea among his successors at the present day, with the corollary that the Evolution of races and species has always been an enormously protracted process. I have myself written many times during the last few years in an opposite sense to this, more especially in three works: *Natural Inheritance*, 1889, in *Finger Prints*, 1892, and in the preface to a reprint of *Hereditary Genius*, 1892.<sup>33</sup>

In *Natural Inheritance*, under a section entitled "Evolution not by Minute Steps Only," Galton stated:

The theory of Natural Selection might dispense with a restriction, for which it is difficult to see either the need or the justification, namely, that the course of evolution always proceeds by steps that are severally minute, and that become effective only through accumulation.<sup>34</sup>

And in *Finger Prints*:

The progress of evolution is not a smooth and uniform progression, but one that proceeds by jerks, through successive

33. Francis Galton, "Discontinuity in Evolution," *Mind*, n.s., 3 (1894): 365, 366.

34. Francis Galton, *Natural Inheritance* (London: Macmillan, 1889), p. 32.

'sports' (as they are called), some of them implying considerable organic changes; and each in its turn being favored by Natural Selection.<sup>35</sup>

Why did Galton break so decisively with Darwin on the issue of discontinuity in evolution? Two reasons are Galton's beliefs in the principle of regression and in the stability of sports. The phenomenon of regression is clear: In a population whose general characters remain constant over a period of generations, each character nevertheless exhibits some variability each generation. Yet the range of this variability does not change from generation to generation. Thus the exceptional members of the population cannot produce even more exceptional offspring, on an average, or else the range of variability of the character in question would expand markedly. Indeed, since those with average characters produce some with exceptional, then the exceptional members must tend to produce less exceptional offspring. In short,

. . . the ordinary genealogical course of a race consists in a constant outgrowth from its centre, a constant dying away at its margins, and a tendency of the scanty remnants of all exceptional stock to revert to that mediocrity, whence the majority of their ancestors originally sprang.<sup>36</sup>

Though not a serious mathematician, Galton was eager to quantify the general laws he observed. Regression fascinated him and he attempted to gather data from which to derive a quantitative law. His data covered the inheritance of size in the sweet pea, and of stature, eye color, temper, artistic faculty, and disease in man. Between 1877 and 1888, Galton published several papers on regression and in 1889 published his book *Natural Inheritance*.

The first six chapters of this book contained discussions of heredity, organic stability, and statistical methods. In the succeeding chapters Galton launched into an analysis of his data. First he treated stature in man:

35. Francis Galton, *Finger Prints* (London: Macmillan, 1892), p. 20.

36. Francis Galton, "Typical Laws of Heredity," *Journal of the Royal Institution* 8 (1875-77): 298.

However paradoxical it may appear at first sight, it is theoretically a necessary fact, and one that is clearly confirmed by observation, that the Stature of the adult offspring must on the whole, be more *mediocre* than the stature of their parents; that is to say, more near to the  $M$  [median or mid-stature] of the general Population.<sup>37</sup>

This of course was the phenomenon of regression.

Galton adopted the following scheme for a quantitative measure of regression. Suppose groups I and II are chosen from a population with a median measure  $M$  of some character. Then the median measure of the character in group I may be expressed as  $M \pm D$ , and in group II as  $M \pm kD$ . The quantity  $k$  Galton defined as the regression of group II on group I with respect to the chosen character. He often expressed  $k$  in other words, saying it was the regression from the group I character to the group II character. Note that when Galton calculates the regression between different generations he must assume that the median  $M$  of the population stays constant from generation to generation.

With his data on stature Galton first converted all female heights to male heights so he could find the average (mid-) height of a group of mixed sexes. He then found that the average regression of mid-filial stature upon mid-parental stature was about  $\frac{3}{5}$ , but he later substituted the value  $\frac{2}{3}$

because the data seemed to admit of that interpretation also, in which case the fraction of two-thirds was preferable as being the more simple expression. . . .

This value of two-thirds will therefore be accepted as the amount of Regression, on the average of many cases, from the Mid-Parental to the Mid-Filial stature, whatever the Mid-Parental stature may be.<sup>38</sup>

In the next paragraph, it becomes clear why Galton considered  $\frac{2}{3}$  the "more simple expression." He wanted to calculate the mid-filial regression on a single parent, but his data were insufficient to calculate the value directly. He adopted the following argument:

37. Galton, *Natural Inheritance*, p. 95.

38. Ibid., p. 98.

### *The Reaction*

As the two parents contribute equally, the contribution of either of them can only be one half of that of the two jointly; in other words, only one half of that of the Mid-Parent. Therefore the average Regression from the Parental to the Mid-Filial Stature must be the one half of two-thirds, or one-third.

The fraction  $\frac{3}{5}$  would not have fit so nicely in this calculation.

Galton summed up his discussion of the law of regression in stature:

The law of Regression in respect to Stature may be phrased as follows; namely, that the Deviations of the Sons from  $P$  [the median stature of the general population] are, on the average, equal to one-third of the deviation of the Parent from  $P$ , and in the same direction. Or more briefly still:—If  $P + (\pm D)$  be the Stature of the Parent, the Stature of the offspring will on the average be  $P + (\pm \frac{1}{3} D)$ .<sup>39</sup>

In the succeeding chapters and appendixes Galton showed that according to his data the same law of regression held for human eye color, the artistic faculty, consumption, and size in sweet peas. He was confident that the law of regression was a theoretical necessity and would be found to hold for nearly all organisms.

Using the basic law of regression of son on father, Galton calculated the regression between more distant relatives than father and son. Since the regression of the son on the father was  $\frac{1}{3}$ , and that of the father on his father was also  $\frac{1}{3}$ , Galton deduced that the regression of the son on the grandfather was  $\frac{1}{3} \times \frac{1}{3} = \frac{1}{9}$ . He similarly derived the regression to be expected between other relatives. For example, to find the regression of nephews on uncles he reasoned: "a Nephew is the son of a Brother, therefore in this case we have [the regression]  $\frac{1}{3} \times \frac{2}{3} = \frac{2}{9}$ ."<sup>40</sup>

Another derivation Galton made from the law of regres-

39. Ibid., p. 104.

40. Ibid., p. 132. Galton's method here is fallacious. It would hold, among other conditions, only if the regressions were entirely independent, which they are not. Pearson has pointed this out in *Galton*, 3A:24.

sion was his later named law of ancestral heredity.<sup>41</sup> He wanted a measure of the separate contribution of each ancestor to a particular character in the offspring. With considerable hand waving<sup>42</sup> he derived the following result:

The influence, pure and simple, of the Mid-Parent may be taken as  $\frac{1}{2}$ , and that of the Mid-Grand-Parent as  $\frac{1}{4}$ , and so on. Consequently, the influence of the individual Parent would be  $\frac{1}{4}$ , and of the individual Grand-Parent  $\frac{1}{16}$ , and so on. It would, however, be hazardous on the present slender basis, to extend this sequence with confidence to more distant generations.<sup>43</sup>

A few pages later Galton stated the law in a different form: "each unit of peculiarity in each ancestor taken singly, is reduced in transmission according to the following average scale;—a Parent transmits only  $\frac{1}{4}$ , and a Grand-Parent only  $\frac{1}{16}$ ."<sup>44</sup>

- Although Galton derived this law from data concerning stature in man, a continuously varying character, he believed it was applicable to nonblending inheritance, such as eye color in humans. Since a parent could not contribute an eye which was one-quarter blue, Galton treated the total heritage as being represented by percentages of the offspring. Thus the eye color of each parent determined on the average the eye color of one-quarter of the offspring. Similarly, the eye color of each grandparent determined the eye color of one-sixteenth of the offspring. Galton used this formulation in his treatment of eye color in chapter 8 of *Natural Inheritance*.

If Galton's derivations of his regression coefficients and his law of ancestral heredity were questionable, he nevertheless opened the door to a statistical analysis of correlations of characters, an analysis which was to have immense influence

41. Pearson named Galton's law of ancestral contributions "Mr. Galton's Law of Ancestral Heredity" in 1898. This development will be treated in the next chapter.

42. See R. G. Swinburne, "Galton's Law—Formulation and Development," *Annals of Science* 21 (1965): 15-31.

43. Galton, *Natural Inheritance*, p. 136.

44. *Ibid.*, p. 138.

upon evolutionary thought. The biometricians were later to point to *Natural Inheritance* as the starting point of biometry.

The implications of regression and the law of ancestral heredity for evolution seemed obvious to Galton. Selection was ineffective in the face of regression "because an equilibrium between deviation and regression will soon be reached, whereby the best of the offspring will cease to be better than their own sires and dams."<sup>45</sup> The extremes which selection caused would quickly be brought back to the center by the action of regression.

Galton made a clear-cut distinction between "sports" and "variations proper," or "mere variations":

The same word 'variation' has been indiscriminately applied to two very different conceptions, which ought to be clearly distinguished: the one is that of the 'sports' just alluded to, which are changes in the position of organic stability, and may, through the aid of Natural Selection, become fresh steps in the onward course of evolution; the other is that of Variation proper, which are merely strained conditions of a stable form of organisation, and not in any way an overthrow of them. Sports do not blend freely together; variations proper do so. Natural Selection acts upon variations proper, just as it does upon sports, by preserving the best to become parents, and eliminating the worst, but its action upon mere variation can, as I conceive, be of no permanent value to evolution, because there is a constant tendency in the offspring to 'regress' towards the parental type.<sup>46</sup>

Looking at the effects of blending inheritance and regression, Galton decided that sports must be the only effective source of evolutionary variation. Darwin, looking at blending inheritance, decided just the opposite—that sports could play no role in evolution. Individual differences must be the effective source of variation for natural selection. Darwin was aware of prepotency but did not believe it was widespread enough to keep sports from being obliterated by blending inheritance. Galton believed that sports were actually quite stable.

45. Galton, *Heredity Genius*, p. 34.

46. Galton, *Finger Prints*, p. 20.

Here then is the basic setting out of which population genetics grew. On the one hand is Darwin's view of gradual and continuous evolution; on the other is Galton's view of abrupt and discontinuous evolution. There were others besides Galton and Huxley who believed in evolution by jumps. Mivart, von Kölleker, and Nägeli were among these, but they all believed in a nonmaterial directive agency guiding the production of large mutations. In 1894 Galton, speaking of his own ideas of discontinuous evolution, was able to say: "These briefly are the views that I have put forward in various publications during recent years, but all along I seemed to have spoken to empty air. I never heard nor have I read any criticism of them, and I believed they had passed unheeded and that my opinion was in a minority of one."<sup>47</sup>

Yet within a year a widely publicized controversy arose about whether evolution was discontinuous or not, and the combating schools both traced their heritage to Galton. This controversy was the prelude to the well-known battle between the Mendelians and biometricians. The origins of that struggle began well before the rediscovery of Mendelian inheritance in 1900.

47. Galton, "Discontinuity in Evolution," p. 369.

## 2

## Background to the Conflict between Mendelians and Biometricians

THE WIDELY PUBLICIZED CONFLICT BETWEEN THE MENDELians and biometricians, which arose soon after the rediscovery of Mendel's work in 1900, influenced the development of population genetics. The conflict caused a split between those who advocated Mendel's theory of heredity and those who advocated Darwin's theory of natural selection. If the Mendelians had worked with, instead of against, the biometricians, the synthesis of Mendelian inheritance and Darwinian selection into a mathematical model, later accomplished by population genetics, might have occurred some fifteen years earlier.

To say the conflict was between the Mendelians and biometricians is misleading, since the basic disagreement was recognized by both parties well before the rediscovery of Mendelian inheritance. The real problem was whether evolution proceeded in general by natural selection operating upon small variations, as Darwin believed, or by discontinuous leaps, as both Huxley and Galton believed. The biometricians supported Darwinian evolution and the Mendelians supported discontinuous evolution.

To understand the background of the conflict, up to the rediscovery of Mendelism, a knowledge of the powerful personalities involved and their interactions is necessary. Although he remained aloof during the conflict proper, Galton was deeply involved, for both sides claimed him as one of their own. The biometricians looked upon Galton as the founder of their new science, and the Mendelians saw him as the father of the theory of evolution by discontinuous leaps. Biometricians Karl Pearson and W. F. R. Weldon and arch-Mendelian William Bateson fought for their ideas with vigor. The intensity of their disagreement generated such strong personal antagonisms that collaboration, which might have been very fruitful, was virtually impossible.

## KARL PEARSON: A SKETCH OF HIS EARLY LIFE

Karl Pearson was born in London in 1857. His father, William Pearson, was a barrister with a strong interest in history. The younger Pearson later said that his father labored diligently on his legal work and "only in the vacations did we really see him; then he was shooting, fishing, sailing with a like energy which astonished me even as an active boy."<sup>1</sup> Pearson resembled his father in the great energy and diligence he focused on his work.

In 1875 Pearson entered King's College, Cambridge, on a scholarship. He graduated with mathematical honors in 1879 and immediately left for Germany, where he studied in Heidelberg and Berlin. In 1880 he returned to London and was called to the Bar in 1881. In 1884, at the age of twenty-seven, he assumed the chair of Applied Mathematics and Mechanics at University College, London, formerly occupied by William Kingdon Clifford.

Pearson himself has described his unusual mixture of intellectual activities during these years:

In Cambridge I studied Mathematics under Routh, Stokes, Cayley, and Clerk Maxwell—but wrote papers on Spinoza. In Heidelberg I studied Physics under Quincke, but also Metaphysics under Kuno Fischer. In Berlin I studied Roman Law under Bruns and Mommsen, but attended the lectures of Du Bois Reymond on Darwinism. Back at Cambridge I worked in the engineering shops but drew up the schedule in Mittel- and Althochdeutsch for the Medieval Languages Tripos. Coming to London, I read in Chambers in Lincoln's Inn, drawing up bills of sale, and was called to the Bar, but varied legal studies by lecturing on Heat at Barnes, on Martin Luther at Hampstead and on Lassalle and Marx on Sundays at revolutionary clubs around Soho. Indeed, I contributed to the Socialist Song Book hymns which I believe are still chanted.<sup>2</sup>

1. Address of Karl Pearson, in *Speeches Delivered at a Dinner Held in University College, London, in Honour of Professor Karl Pearson, 23 April 1934* (privately printed, Cambridge: Cambridge University Press, 1934), p. 20.

2. Ibid.

After returning from Germany, Pearson gave many lectures on German culture, dealing especially with the life and times of Martin Luther. He wrote a treatise in German on engravings of Jesus Christ during the Middle Ages, composed a nineteenth-century passion play, produced reviews on the works of Spinoza, and wrote a large number of other letters, articles, and reviews. In addition, he published several very technical papers, for example, "On the Motion of Spherical and Ellipsoidal Bodies in Fluid Media."<sup>3</sup> He also assumed the difficult task of editing Clifford's *Common Sense of the Exact Sciences* and Isaac Todhunter's *A History of the Theory of Elasticity and of the Strength of Materials from Galilei to the Present Time*. Both of these important works required considerable effort to complete. Besides his writing, Pearson devoted much time to his professional duties, lecturing on geometry and mechanics. Students found him stimulating.

Pearson was an intelligent young man. He knew it, and was quick to criticize the incompetence of others. An example was his attack on an exhibition in 1883 at the British Museum celebrating the three hundredth anniversary of Martin Luther's birth. When others reacted to his criticism, he engaged in a number of literary duels, brandishing sharp-edged rhetoric. Henry Bradshaw, Pearson's most respected and admired teacher, wrote him the following letter concerning these exchanges:

I have not the slightest wish to defend the Museum ignorance. But . . . when a man who might by his own deeper knowledge help to make such an exhibition very much more interesting and instructive wastes his energies in writing to the *Athenaeum* as you do, it naturally produces the impression that his main object is to let the world see how much more he knows of the subject than the idiots to whose care he says these treasures are entrusted. Those who know you know also that that is not the object you have in view, but it is a pardonable inference for ordinary people to draw. Everything you write about this shows such an extraordinary absence of

3. *Quarterly Journal of Pure and Applied Mathematics* 20 (1883): 60–80.

wisdom (by which I don't mean knowledge or cleverness, both of which are abundantly shown). . . .<sup>4</sup>

Pearson allowed this letter to be published in a memoir of Bradshaw in 1888, which indicates he took the criticism to heart. He was still quick, however, to discredit prime examples of sloppy thinking. Later he assigned significant portions of William Bateson's thought to this category.

In 1889, Pearson was much influenced by reading Galton's *Natural Inheritance*. Looking back in 1934, Pearson quoted from Galton's Introduction:

"This part of the enquiry may be said to run along a road on a high level, that affords wide views in unexpected directions, and from which easy descents may be made to totally different goals to those we have now to reach."

Pearson went on to say:

"Road on a high level," "wide views in unexpected directions," "easy descents to totally different goals"—here was a field for an adventurous roamer! I felt like a buccaneer of Drake's days—one of the order of men "not quite pirates, but with decidedly piratical tendencies," as the dictionary has it! I interpreted that sentence of Galton to mean that there was a category broader than causation, namely correlation, of which causation was only the limit, and that this new conception of correlation brought psychology, anthropology, medicine and sociology in large parts into the field of mathematical treatment. It was Galton who first freed me from the prejudice that sound mathematics could only be applied to natural phenomena under the category of causation. Here for the first time was a possibility—I will not say a certainty of reaching knowledge—as valid as physical knowledge was then thought to be—in the field of living forms and above all in the field of human conduct.<sup>5</sup>

Pearson was obviously influenced by *Natural Inheritance*. His first lecture on inheritance was given shortly after its publication and consisted of an exposition and amplification

4. Quoted in Egon Sharpe Pearson, *Karl Pearson* (Cambridge: Cambridge University Press, 1938), p. 7.

5. Pearson, in *Speeches*, pp. 22-23.

of Galton's views.<sup>6</sup> At this time he was editing the second volume of Todhunter's *History of the Theory of Elasticity* (published 1893) and formulating the views of methodology in his influential *Grammar of Science* (published 1892). But Pearson's interest in evolution, heredity, and statistics was becoming stronger. When the biologist W. F. R. Weldon was appointed to University College in 1891, he exerted a strong influence on Pearson, whose work was then redirected toward a furtherance of Galton's efforts. Weldon was looking for someone like Pearson to help him.

#### WELDON, PEARSON, AND BIOMETRY

Walter Frank Raphael Weldon was born in 1860. He studied botany and zoology one year at the University of London with Daniel Oliver, Ray Lankester, and A. H. Garrod, intending to enter the medical profession. In 1878 he went to St. John's College, Cambridge, and began to study with the young morphologist, Francis Balfour, who greatly influenced him.

Following the lead of von Baer and Haeckel, Balfour believed that the development of the individual recapitulated the history of the species and that evolutionary relationships were often best revealed by a comparative study of embryological development rather than of adult stages. Balfour's ability was recognized early. He was elected to the Royal Society at age twenty-seven and published his influential *Comparative Embryology* in 1881. Balfour was concerned with elucidating the relationships between groups of animals, especially those which lay in the amorphous region between the vertebrates and invertebrates.

The excitement of pursuing Darwin's ideas into the embryological realm was a great inducement to all of Balfour's students, and Weldon became eager to follow in his steps. He was even given the privilege of working as demonstrator

6. Karl Pearson, "Walter Frank Raphael Weldon, 1860-1906," *Biometrika*, 5 (1906): 16, n.

for Balfour one term. Unfortunately, Balfour was killed in an Alpine accident in 1882, at age thirty-one.

Adam Sedgwick, formerly Balfour's demonstrator, was appointed to Balfour's chair and invited Weldon to demonstrate for him. Weldon soon finished his first published paper, on the early development of *Lacerta muralis*, a lizard. Several other papers on embryology followed, and in 1884 he was appointed University Lecturer in Invertebrate Morphology at St. John's. Many of Weldon's students became biologists. Among them was William Bateson.

Beginning in 1888 Weldon's interest began to turn from morphology to problems in variation and organic correlation. For example, he had observed that evolutionary changes in adults of some species were accompanied by changes in the larval forms; yet the new adult characters and the new larval characters had no apparent connection. Weldon suspected a correlation existed but did not know how to prove it. Although he was an accomplished morphologist, he became convinced that the analysis of evolution by strictly morphological methods was inadequate.

In 1889, Galton's *Natural Inheritance* furnished Weldon what he was seeking—a quantitative method of attacking organic correlation and the problems of variation. He immediately set to work with elaborate measurements of Decapod Crustacea and found the distribution of variations very similar to that found by Galton in man. His paper, entitled "The Variations Occurring in Certain Decapod Crustacea: 1. *Crangon vulgaris*,"<sup>7</sup> was submitted to the Royal Society with Galton as referee. Galton encouraged Weldon and helped him revise the rather primitive statistical treatment. This marked the beginning of a long friendship.

In his next paper, "On Certain Correlated Variations in *Crangon vulgaris*,"<sup>8</sup> Weldon attempted to measure numerically the amount of interrelation between characters in the same individual, that is, the correlation coefficient. He believed that the correlation coefficient between two organs or

7. *Proceedings of the Royal Society* 47 (1890): 445-53.

8. *Ibid.*, 51 (1892): 2-21.

characters would be constant for a given species (or at least races of species) and would clarify the "functional correlations between various organs which have led to the establishment of the great sub-divisions of the animal kingdom."<sup>9</sup> In other words, the evolutionary relationships which traditional morphology had attempted to demonstrate might be better demonstrated by appropriate statistical studies of populations. Weldon stated in a third paper:

It cannot be too strongly urged that the problem of animal evolution is essentially a statistical problem: that before we can properly estimate the changes at present going on in a race or species we must know accurately (a) the percentage of animals which exhibit a given amount of abnormality with regard to a particular character; (b) the degree of abnormality of other organs which accompanies a given abnormality of one; (c) the difference between the death rate per cent in animals of different degrees of abnormality with respect to any organ; (d) the abnormality of offspring in terms of the abnormality of parents and *vice versa*. These are all questions of arithmetic; and when we know the numerical answers to these questions for a number of species, we shall know the deviation and the rate of change in these species at the present day—a knowledge which is the only legitimate basis for speculations as to their past history, and future fate.<sup>10</sup>

With these words Weldon formulated the basic principles of the biometrical approach derived from Galton. He did not, however, know enough mathematics to develop the needed methods, so he began a study of French mathematicians who wrote on probability and attempted to interest a mathematician in his work. From his studies Weldon became an adequate but certainly not brilliant statistician. Far more important, he attracted the attention of Karl Pearson, who developed the basic methods for the statistical study of populations.

Weldon came to University College, where Pearson was teaching, in 1891. Pearson describes their animated conversations:

9. *Ibid.*, p. 11.

10. "On Certain Correlated Variations in *Carcinus moenas*," *Proceedings of the Royal Society* 54 (1893): 329.

[we] both lectured from 1 to 2, and the lunch table, between 12 and 1, was the scene of many a friendly battle, the time when problems were suggested, solutions brought, and even worked out on the back of the menu or by aid of pellets of bread. Weldon, always luminous, full of suggestions, teeming with vigor and apparent health, gave such an impression to the onlookers of the urgency and importance of his topic that he was rarely, if ever, reprimanded for talking "shop."<sup>11</sup>

Weldon's enthusiasm was contagious and Pearson became very interested in the problems of evolution. When he had finished work on the *Grammar of Science* and the second volume of Todhunter's *History of the Theory of Elasticity*, Pearson began to devote much of his thought to evolution. His first paper<sup>12</sup> came as a response to a problem uncovered by Weldon, who had found that the relative frontal breadth in the shore crab did not follow a Gaussian distribution whereas the distributions of other characters of the crab were normal. Weldon hypothesized, and Pearson showed mathematically, that relative frontal breadth must be dimorphic, each form representing a race. In this paper Pearson developed the method of moments for fitting a theoretical curve to observational data; in later years his methods for doing this became more sophisticated.

By late 1893, Weldon and Galton had become good friends. Galton was impressed by Weldon's early papers, and both were interested in discovering other dimorphic characters. Weldon had also begun experiments attempting to measure the selective death rate in several different species. In December of 1893, Galton and Weldon, with several others, worked out a proposal to the Royal Society for the establishment of a committee to further their work. Weldon naturally assumed that the committee would provide some funds and facilities for research, as well as a convenient means of publication. The committee was approved with Francis Galton as chairman and Weldon as secretary. Francis Darwin, A. Macalister, R. Medola, and E. B. Poulton were the other members. The committee was entitled Committee for Conducting Statistical

11. Pearson, "Weldon," p. 18.

12. "Contributions to the Mathematical Theory of Evolution," *Philosophical Transactions of the Royal Society* 185, A (1894): 70-110.

Inquiries into the Measurable Characteristics of Plants and Animals, and it was suggested that a statistician should be added later.

The committee at first seemed to be a great boon for Weldon. He believed the possibilities for extending his researches were boundless, and he set to work with great enthusiasm. Pearson stated that Weldon at this time "wanted the whole mathematical theory of selection, the due allowances for time and growth, the treatment of selective death-rates and the tests of heterogeneity and dimorphism settled in an afternoon's sitting."<sup>13</sup> But as the committee's work progressed, Weldon found the situation far less conducive to research than he had first imagined.

Weldon was unable to distinguish the possible tasks from the impossible, and he felt acutely the lack of powerful mathematical methods, developed only later by Pearson. For example, Weldon attempted to distinguish the subraces of ox-eyed daisies by examining the ray florets. When the material produced strikingly irregular frequency distributions, Weldon was at a complete loss to analyze the data. Also, typical of any committee of the Royal Society, pressure existed to produce solid work rather than tentative conclusions. Weldon therefore had to give up plans for some of his projected researches.

A more basic problem was a disagreement between Galton and Weldon on whether evolution was continuous or discontinuous. As described above, Galton firmly believed that evolution proceeded by jumps, and he expressed this view clearly in 1894 as well as earlier. On the other hand, Weldon and Pearson, both confirmed Darwinists, believed that evolution proceeded by selection operating upon continuous differences. Pearson expressed his belief in the essential gradualness of evolution as early as 1883,<sup>14</sup> and Weldon appears to have become fixed in this belief by the time of his first statistical paper in 1890. The statistical methods used by Pearson and Weldon were particularly suited to the study of continuous variation.

Here then is the paradox. Pearson and Weldon, viewing

13. Pearson, "Weldon," p. 24.

14. E. S. Pearson, *Karl Pearson*, p. 13.

Galton as the founder of the methods of the biometrical school, believed they were following in his footsteps. But they also believed in continuous evolution, while Galton's reasoning, in Pearson's words, "left him practically in the ranks of the mutationists—a strangely inconsistent position for one who has been looked upon as the founder of the Biometric School!"<sup>15</sup>

How did Pearson and Weldon justify their position? Galton's reason for believing in discontinuous evolution has been stated already: the force of regression was so powerful that selection of continuous variations could have only a limited effect; therefore, evolution must proceed by large stable jumps. Pearson and Weldon claimed that Galton simply misinterpreted his own valid methods. Regression did not quash all exceptional variation of the blending sort, *if the exceptional offspring were bred among themselves*. Pearson stated:

The flaw in Galton's argument is . . . that he is overlooking the fact that he has clubbed together parents of all possible types of ancestry, and the "regression" of his sons is solely due to the large number of such parents who have sprung from an ancestry mediocre or below mediocrity. The amount of filial regression depends entirely on the amount of this mediocrity, and there will be no regression if two or three generations above the parents are of like deviation from mediocrity. Thus, although it may still be a matter for experiment and discussion, whether evolution proceeds by variations proper or by spurts, whether it be continuous or advance by jerks, the reason which made Galton the pioneer in advocating discontinuous evolution was a misinterpretation of his own discovery of "regression."<sup>16</sup>

Thus Pearson believed that he and Weldon were following the true Galtonian methods in dealing with evolution, while Galton himself was led astray by bad reasoning. Wilhelm Johannsen later produced new evidence which appeared to contradict Pearson's reasoning and claimed that the true Galtonian method necessarily led to a belief in the discontinuity of evolution (see chap. 4).

15. Pearson, *Galton*, 3A:86.

16. *Ibid.*, p. 79.

Galton differed markedly from Weldon on the interpretation of the process of evolution. Both wanted the committee to study dimorphic forms, but Galton did not think one form could be continuously selected into another and Weldon did. Galton saw each of the dimorphic forms as a stable center which resisted the influence of selection. Weldon did not see any significant obstacle to selection. The outcome of this difference was not a personal quarrel but could be seen in the way Galton shaped the aims of the committee.

In 1895, Weldon published a paper which formed part of the first report of the committee. It was entitled "Attempt to Measure the Death-rate Due to the Selective Destruction of *Carcinus moenas* with Respect to Particular Dimension."<sup>17</sup> Weldon tried to demonstrate that the death rate was correlated with a measurable character of the shore crab. If this were true, the Darwinian theory of gradual evolution by the selection of continuous differences would be demonstrated.

Galton could have hardly agreed with Weldon's conclusions. He needed to say nothing, however, because William Bateson entered vociferously into a sharp criticism of Weldon's methods and conclusions. Bateson considered it a disgrace that Weldon should be allowed to publish such papers under the auspices of a committee of the Royal Society and made his views known to Galton in a series of long letters. From this time on Bateson was inextricably involved with the committee and, more than any other individual, shaped its future work.

#### WILLIAM BATESON AND DISCONTINUOUS EVOLUTION

William Bateson was born in 1861. His father, Dr. William Henry Bateson, was forty-nine years old at the time and master of St. John's College, Cambridge, a post he filled until his death in 1881. Young William was not very happy and did poorly in school. At age fourteen he went to Rugby, a preparatory school. Later, Bateson's wife had this to say:

But in spite of his very evident ability, Will was no success at school. Quarter after quarter his school reports express the

17. *Proceedings of the Royal Society* 57 (1895): 360-79.

dissatisfaction and disappointment of his masters, and his name figures ominously near the bottom of all his class lists. He was unpopular among the boys. Probably his intense and emotional sensitiveness, combined with an unusually alert critical faculty, made him an object of dislike to his school-fellows, and made his masters objects of dislike to him.<sup>18</sup>

Bateson himself wrote his mother during his stay at Rugby:

Is anyone happy? I don't think I shall be. You will say, this is all morbid nonsense, but it is true. I never get on with anybody for long; at home even I am always in some scrape except when I am alone. And don't please write back that I am foolish and that, and then not tell me how to cure it.<sup>19</sup>

Even when Bateson was successful in his field, he retained his sensitivity to criticism and responded quickly and sharply to his critics.

In 1879, Bateson left Rugby and entered St. John's College, where his father was still master. The mathematics portion of the elementary matriculation exam gave him trouble:

Mathematics were my difficulty. Being destined for Cambridge, I was specially coached in mathematics at school [Rugby]. Arrived here [St. John's], I was again coached, but failed. Coached once more I passed, having wasted, not one, but several hundred hours on that study.<sup>20</sup>

Bateson never became competent in mathematics—a sore point in his later controversy with the biometrists.

At St. John's, however, Bateson was a successful student. He graduated in 1883 after placing first in both parts of the Natural Sciences Tripos. W. F. R. Weldon, who entered one year before Bateson, was at St. John's at this time studying embryology. Mrs. Bateson states that in 1883 Weldon was Bateson's "most intimate friend,"<sup>21</sup> and Weldon was instrumental in getting Bateson interested in the wormlike *Balanoglossus*. Weldon not only gave Bateson access to his own col-

18. Beatrice Bateson, *William Bateson, F.R.S. Naturalist* (Cambridge: Cambridge University Press, 1928), pp. 4-5.

19. *Ibid.*, p. 5.

20. *Ibid.*, p. 10.

21. *Ibid.*, p. 17, n.

lections but also helped him get permission to study with Professor W. K. Brooks of Johns Hopkins University during the summers of 1883 and 1884. *Balanoglossus* was abundant in Chesapeake Bay. Despite the friendship, a sour note prophetic of the future was later revealed by Bateson, who said he was "often made to feel like Weldon's bottle-washer"<sup>22</sup> during his student days.

Bateson's careful study of *Balanoglossus*, an animal which had been previously classified as an Echinoderm, was his only research in traditional morphology. He published three descriptive papers; then in a fourth entitled "The Ancestry of the Chordata,"<sup>23</sup> he discussed the significance of his work. In a boldly conceived argument, Bateson showed that segmentation, which *Balanoglossus* lacked, was not a basic characteristic of the chordates, and that in other respects the animal should be considered a primitive member of Chordata. He then elucidated the relationship of *Balanoglossus* and its allies to the other chordates. His argument was a classic example of the application of Balfour's embryological method and was widely incorporated into textbooks.

But Bateson was already growing beyond Balfour's method. Even as he wrote the paper on the ancestry of the Chordata, he stated his reservations:

The decision that it would be profitable to analyse the bearing of the new fact in the light of modern methods of morphological criticism, does not in any way prejudge the question as to the possible or even probable error in these methods.

Of late the attempt to arrange genealogical trees involving hypothetical groups has come to be the subject of some ridicule, perhaps deserved. But since this is what modern morphological criticism in great measure aims at doing, it cannot be altogether profitless to follow this method to its logical conclusions.

22. Recorded by R. C. Punnett, "Early Days of Genetics," *Heredity* 4 (1950): 2.

23. *Quarterly Journal of Microscopical Science* 26 (1886); reprinted in R. C. Punnett, ed., *Scientific Papers of William Bateson*, 2 vols. (Cambridge: Cambridge University Press, 1928), 1:1-31 (hereafter cited as *Scientific Papers*).

That the results of such criticism must be highly speculative, and often liable to grave error, is evident.<sup>24</sup>

Mrs. Bateson notes that within two years her husband "outgrew the *Balanoglossus* work and came even to regard it as trifling."<sup>25</sup>

Bateson, as did Weldon when he became disenchanted with Balfour's work, turned to the study of variation as the key to the unsolved problems of evolution. It was probably Brooks who guided Bateson's interests in this direction. During the summers of 1883 and 1884, Bateson and Brooks engaged in long conversations about variation and the mechanism of evolution. Mrs. Bateson said that her husband "delighted in recalling the long hours of discussion (Brooks lying in his shirt-sleeves on his bed and Will sitting by), when problem and theory and practice passed in long review with ever fresh interest."<sup>26</sup> In 1883, Brooks was just finishing his book *The Law of Heredity: A Study of the Cause of Variation and the Origin of Living Organisms*, in which he proposed a new theory of heredity to supplant Darwin's pangenesis. His theory of heredity allowed for saltation variation and discontinuous evolution. In the section entitled "Saltatory Evolution," Brooks cites the arguments of Huxley, Galton, and Mivart concerning saltation evolution, then gives a series of examples of new races being formed by sudden jumps. He concludes:

These cases show us that very considerable variations may suddenly appear in cultivated plants and domesticated animals, and that these sudden modifications may be strongly inherited, and may thus give rise to new races by sudden jumps.

The analogy of domesticated forms would lead us to believe that the same thing sometimes occurs in nature, and that Darwin has over-estimated the minuteness of the changes in wild organisms, and has thus failed to see that natural selection may give rise to new and well-marked races in a few generations.<sup>27</sup>

24. *Ibid.*, p. 1.

25. B. Bateson, *William Bateson*, p. 18.

26. *Ibid.*

27. W. K. Brooks, *The Law of Heredity: A Study of the Cause of Variation and the Origin of Living Organisms* (Baltimore: John Murphy, 1883), pp. 301-2.

In another section Brooks treated the significance of serial homology and symmetry. The issues raised by Brooks—discontinuity in evolution, symmetry in organisms, and heredity—became the major problems upon which Bateson focused his life work.

Immediately upon finishing his paper on Chordata in the spring of 1886, Bateson left for Russia to investigate the relation between the variations of animals and their environments. His method was to choose environments which differed clearly in some measurable characteristic and to see if variations were correlated with the differences in conditions. The small isolated lakes of different salinity on the Russian steppes seemed ideal sites to test such correlations. He found no general rule: some animals had characters which were uniformly affected by a change in conditions, whereas other animals were entirely unaffected. Thus the evolutionary effects of a change in conditions did not seem as clear to Bateson as it had to Darwin.

Furthermore, in the best example of an animal which did show a correlated alteration with a change in conditions, Bateson thought the animal might revert to its original form if put back into the original environment:

Upon this point I have no evidence; but that the animals would, if they lived and propagated, ultimately regain their former structure appears probable; for, since it can be shown that certain variations are constantly produced by water of certain constitution, it practically follows that the maintenance of these variations depends also on the same cause.<sup>28</sup>

If this were the case, the correlated variations would have negligible evolutionary significance—no permanent changes could be effected. Bateson found little on his trip to indicate that the natural selection of Darwin's "individual differences" had produced new and permanent species.

Bateson regarded his expedition to Russia, and a later

28. William Bateson, "On Some Variations of *Cardium edule* Apparently Correlated to the Conditions of Life," *Philosophical Transactions of the Royal Society*, B, 180 (1889), reprinted in *Scientific Papers*, 1:34.

shorter one to Egypt, as failures.<sup>29</sup> He had discovered no definite connection between the environment and correlated variations. But his failure stimulated him to search for better information about variation. On the basis of his morphological work, Bateson was elected to the Balfour Studentship in November 1887. Ironically, by the time the studentship was awarded to him, Bateson had become thoroughly disenchanted with Balfour's morphological approach, and he used the Studentship to attack the problem of evolution by the study of variation.

Bateson was appalled by the lack of information about variations of plants and animals. He rightly believed that modern researchers had scarcely moved beyond Darwin's work in this field, and he set out to remedy the situation. At first he simply wanted to gather all the data on variation that he could and publish it. Each person could then draw his own conclusions about the mechanism of evolution from the data.

Since the Balfour Studentship provided few funds for research, Bateson applied in 1890 for the Linacre Professorship in Comparative Anatomy at Oxford. He knew that the position would almost certainly be offered to Ray Lankester, but in case Lankester should refuse, Bateson wanted to offer his new approach to the problems of evolution. His letter of application states clearly his aims at the time. He rejected anew the embryological method of von Baer and Balfour which he said "rests on an error in formal logic."<sup>30</sup> That ontogeny reproduces phylogeny was not a valid assumption. Instead, Bateson declared, variation was the key to evolution. The letter of application made Bateson appear a Darwinian. Indeed, he said the purpose of his research was to "pursue Darwin's problems and to employ Darwin's methods."<sup>31</sup>

29. Mrs. Bateson states that her husband "always regarded these expeditions as failures and regretted that in his inexperience he had undertaken the investigation with too definite and narrow expectation, and had pursued the inquiry too closely to profit by the large opportunity of general observation" (*William Bateson*, p. 27).

30. *Ibid.*, p. 32.

31. *Ibid.*, p. 35.

But already Bateson had become dissatisfied with the study of continuous variations, Darwin's "individual differences." His teacher and friend Brooks had suggested the importance of discontinuous variation. His travels and further research had indicated that evolutionary changes were not directly connected to selection pressures caused by differences in environment acting upon continuous variations. Thus his interest was led inexorably toward the larger, discontinuous variations. By the time of his application for the Linacre Professorship, Bateson was already convinced that in repeated parts, such as fingers or teeth, large variations played a crucial role in evolution. He knew this was distinctly un-Darwinian, but in his application merely said that the importance of the facts he had collected about variation of repeated parts "lies in their value as evidence of the magnitude of the integral steps by which variation proceeds. . . ."<sup>32</sup> Bateson did not want his application to appear un-Darwinian.

As expected, Lankester was appointed Linacre Professor. Bateson felt less restraint to conceal his attitude and began publishing a series of papers on large discontinuous variations. In the first paper, still hesitant to make the break with Darwinism, he declined the rather obvious temptation to draw inferences from the data to the mechanism of evolution: "Though one is naturally tempted to draw seemingly obvious deductions from the facts about to be given, it is not proposed on the present occasion to do more than describe the actual structures as they are found."<sup>33</sup> In the next paper, however, entitled "On the Variations in Floral Symmetry of Certain Plants Having Irregular Corollas,"<sup>34</sup> the break is stated clearly.

In the Introduction, Bateson made it clear that he believed Darwin's theory to be impossible. "It is difficult," he said, "to suppose both that the process of Variation has been a con-

32. *Ibid.*, p. 36.

33. William Bateson, "On Some Cases of Abnormal Repetition of Parts of Animals," *Proceedings of the Zoological Society* (1890); reprinted in *Scientific Papers*, 1:113.

34. *Journal of the Linnaean Society* (Bot.), 28 (1891); reprinted in *Scientific Papers*, 1:126-61.

tinuous one; and also that Natural Selection has been the chief agent in building up the mechanisms of things."<sup>35</sup> In the shaping of a new character, the small variations which Darwin postulated would be of such small, if any, selective value that natural selection would be ineffective. This was, of course, an old criticism of Darwin's theory, but Bateson believed it to be a real one.

The primary point of the article was to show that discontinuous variations did in fact exist, and in consequence

that in proportion as the process of Evolution shall be found to be discontinuous the necessity for supposing each structure to have been gradually modelled under the influence of Natural Selection is lessened, and a way is suggested by which it may be found possible to escape from one cardinal difficulty in the comprehension of Evolution by Natural Selection.<sup>36</sup>

Bateson concluded that the facts of discontinuous variation presented in the article, while few, "are a sample of the kind of fact which is required to enable us to deal with the problems of Descent."<sup>37</sup>

The moment Bateson broke from Darwinism he also broke from Weldon. Their training in biology had been similar, both being strongly influenced by Balfour. Both rejected the morphological approach and began a study of variation as the key to evolution. But Weldon stayed with Darwin's view of evolution by natural selection of small differences, while Bateson, disillusioned by this approach, adopted the view that evolution proceeded by discontinuous leaps. Bateson was certainly aware of the break he was making with tradition, and once the decision was made, he defended his position with alacrity.

Bateson found support in the ideas of Francis Galton. He had been corresponding with Galton since the publication of *Natural Inheritance* and had sent Galton offprints of his papers. Bateson later said of Galton:

35. Ibid., p. 128.

36. Ibid.

37. Ibid., p. 150.

The novelty of his thoughts and the freshness of his outlook on nature are not to be found in any other living writer, so far as I know. I often remember the thrill of pleasure with which I first read *Hereditary Genius* and the earlier chapters of *Natural Inheritance*.<sup>38</sup>

In the article on floral symmetry where Bateson made his break with Darwinism clear, the similarity of his ideas to those expressed by Galton in *Natural Inheritance* is striking. Bateson states there are two classes of variation: the continuous, exemplified by the variations studied by Galton in man and by Weldon in shrimp, and the discontinuous, some examples of which he had just presented. The distinction Bateson makes between continuous and discontinuous variation is precisely the distinction Galton makes between "sports" and "variation proper." Bateson also uses Galton's notion of equilibrium in making the distinction. The intermediate forms between two discontinuous variations, where symmetry was involved, were "points of unstable equilibrium."<sup>39</sup> Bateson concluded with a statement which sounded like Galton:

If . . . as may be alleged, there is little evidence that species may arise by what may be called discontinuous Variation—a Variation in kind—there is still less evidence that new forms can arise by those Variations in degree which at any given moment are capable of being arranged in a curve of Error, and no one as yet has ever indicated the way by which such Variations could lead to the constitution of new forms, at all events under the sole guidance of Natural Selection.<sup>40</sup>

There can be little doubt that Bateson was influenced by his reading of *Natural Inheritance*.

In 1894, Bateson published his huge *Materials for the Study of Variation, Treated with Especial Regard to Discontinuity in the Origin of Species*.<sup>41</sup> He presented 886 cases of discontinuous variation and expanded his views on discontinuity in

38. Bateson to Miss Evelyn Biggs (great-niece of Francis Galton), 7 July 1909, in Pearson, *Galton*, 3A:288.

39. Bateson, *Scientific Papers*, 1:158.

40. Ibid., p. 159.

41. London: Macmillan, 1894.

evolution. Galton gave the book an enthusiastic welcome. After stating that he himself had propounded similar views for many years, which had gone unheard, Galton continued:

It was, therefore, with the utmost pleasure that I read Mr. Bateson's work bearing the happy phrase in its title of "discontinuous variation," and rich with many original remarks and not a few trenchant expressions.<sup>42</sup>

Bateson also sent a copy of the book to Huxley, who wrote back:

I see you are inclined to advocate the possibility of considerable "saltus" on the part of Dame Nature in her variations. I always took the same view, much to Mr. Darwin's disgust, and we used often to debate it.<sup>43</sup>

Both Galton and Huxley clearly approved of Bateson's emphasis upon discontinuity in evolution.

Weldon's response to *Materials* was less enthusiastic. He did not believe evolution was discontinuous. He questioned Bateson's claim that a discontinuous variation was a new center of organic stability and not subject to regression. Galton had, of course, made the same claim earlier. Weldon stated in a letter to Bateson:

About "regression," I will say only this, that Galton was himself a good deal mixed, at least in his exposition, when he wrote *Natural Inheritance*: and that I cannot conceive that characters "which do not mix" are thereby rendered independent of the phenomenon of regression.<sup>44</sup>

Although Weldon and Bateson disagreed on the issue of continuity in evolution, their correspondence at this time, early 1894, shows nothing of the personal antagonisms which would soon be evident.

On 10 May 1894, Weldon's review of *Materials* appeared in *Nature*. First he praised the book:

42. Galton, "Discontinuity in Evolution," p. 369.

43. T. H. Huxley to Bateson, 20 February 1894, in L. Huxley, *Life and Letters of Thomas Henry Huxley*, 2:394.

44. Weldon to Bateson, 15 February 1894, Bateson Papers, Baltimore, no. 13. A collection of Bateson papers is on microfilm at the American Philosophical Society, Philadelphia. The society furnishes a guide to the number system. The Bateson Papers are cited hereafter as BPB.

The whole work must be carefully read by every serious student; there can be no question of its great and permanent value, as a contribution to our knowledge of a particular class of variations, and as a stimulus to further work in a department of knowledge which is too much neglected.<sup>45</sup>

But then he launched into a sharp criticism of Bateson's interpretation of his data, especially his emphasis upon discontinuity in evolution. He challenged Bateson's contention that species were more discontinuous than the environments which produced them and attacked his treatment of discontinuous variation. The resulting impression was that Bateson had done well to study the problem of variation as connected with evolution but that his ideas of discontinuity in variation and evolution were misguided, as was his method of research. Weldon suggested Bateson should drop his idea of discontinuity and adopt biometrical methods for the study of variation.

Pearson's interpretation was that this review signaled the beginning of Bateson's attacks upon Weldon.<sup>46</sup> Certainly Bateson was provoked by the review. To make matters worse, *Materials* sold poorly. It ran against the grain of Darwinism, which was popular in England at this time. Galton had already received the cold shoulder with his ideas on discontinuous evolution. But Bateson was eager to challenge the orthodox school, and a series of confrontations began between Bateson and the Darwinians, especially Weldon. Within a year of Weldon's review, he and Bateson were engaged in a heated public controversy. They were to cease fighting only with Weldon's death in 1906.

#### THE PUBLIC CONTROVERSIES

##### THE CINERARIA CONTROVERSY

The first public controversy between Bateson and the Darwinists was over the origin of cultivated Cineraria. At a meeting of the Royal Society on 28 February 1895, the biologist W. T. Thiselton-Dyer exhibited two forms of Cineraria: the wild type *C. cruenta* from the Canary Islands and a re-

45. W. F. R. Weldon, "The Study of Animal Variation," *Nature* 50 (1894): 24.

46. Pearson, *Galton*, 3A:287.

cently cultivated form from the Royal Gardens at Kew. The two varieties differed markedly in the shape and color of the flowers. Dyer claimed that the cultivated form was derived from the wild type by artificial selection of continuous differences. In a letter to *Nature* published on 14 March 1895, Dyer clarified his remarks at the meeting. He minimized the value of sports in evolution: "As I conceive the [evolutionary] process, it is one of continuous adjustment of 'slight' variations on one side and the other."<sup>47</sup> As an example of a change which had been accomplished by the gradual accumulation of small variations, he referred to the change from *C. cruenta* to the modern Cineraria.

Bateson did not attend the meeting but he read Dyer's letter. Here was his chance to challenge the prevalent Darwinian view of evolution. After making a study of horticultural records, he concluded in a letter published in *Nature*:

The foregoing notes of history must, I think, be taken to show (1) that the modern Cinerarias arose as hybrids derived from several very distinct species; (2) that the hybrid seedlings were from the first highly variable; (3) that 'sports' of an extreme kind appeared after hybridization in the early years of the 'improvement' of these plants; (4) that the subsequent perfection of the form, size and habit has proceeded by a slow process of selection. Mr. Dyer's statement that the modern Cinerarias have been evolved from the wild *C. cruenta* 'by the gradual accumulation of small variations' is therefore, in my judgment, misleading, for this statement neglects two chief factors in the evolution of the Cineraria, namely, hybridization and subsequent 'sporting.'<sup>48</sup>

The controversy now began in earnest. Ten additional letters concerning Cineraria were published by *Nature* during the next two months. First, Dyer and Bateson again exchanged letters. Dyer<sup>49</sup> challenged Bateson's belief that hybridization was important in the evolution of the new form of Cineraria because it, like *C. cruenta*, was herbaceous. The other Cinerarias which Bateson claimed were hybridized with

47. *Nature* 51 (1895): 461.

48. Letter from William Bateson, 25 April 1895, *ibid.*, p. 607.

49. Letter from W. T. Thiselton-Dyer, 29 April 1895, *Nature* 52 (1895): 3-4.

*C. cruenta* to form modern Cineraria were shrubby species. Since modern Cineraria was herbaceous and had leaves like *C. cruenta*, Dyer claimed that modern Cineraria arose directly from *C. cruenta*. Bateson replied that Dyer had not disproved his contention that the change was discontinuous, and that the question of the hybrid origin of cultivated Cineraria was "of subordinate interest"<sup>50</sup> compared to the question of discontinuity. Furthermore, Dyer's claim against the hybrid origin of modern Cineraria was, said Bateson, directly contradicted by the horticultural literature.

Weldon now entered the fray with an attempt to discredit Bateson's position. His argument was that Bateson had misused his source materials: "I . . . wish to point out that Mr. Bateson has omitted from his account of these records some passages which materially weaken his case. . . . All I wish to show is that the documents relied upon by Mr. Bateson do not demonstrate the correctness of his views; and that his emphatic statements are simply of want of care in consulting and quoting the authorities referred to."<sup>51</sup>

Bateson thought Weldon had initiated a personal attack. They arranged to meet on 21 May 1895 to discuss the issue. During the conversation Bateson understood Weldon to say that Dyer was bluffing. Bateson's recorded notes of the conversation state: "Weldon's position, in writing is therefore that of the accomplice who creates a diversion to help a charlatan. I cannot at all understand his motives, or how he can bring himself to play this part."<sup>52</sup> Weldon's position was made clear in a letter to Bateson three days later:

24 May 1895

Dear Bateson,  
I can do no more.

First, you accuse me of attacking your personal character; and when I disclaim this, you charge me with a dishonest defense of some one else.

I have throughout discussed only what appeared to me to be facts, relating to a question of scientific importance.

50. Letter from William Bateson, 9 May 1895, *ibid.*, p. 29.

51. Letter from W. F. R. Weldon, 13 May 1895, *ibid.*, p. 54.

52. BPB 10.

If you insist upon regarding any opposition to your opinions concerning such matters as a personal attack upon yourself, I may regret your attitude, but I can do nothing to change it.

Yours very truly,  
W. F. R. Weldon<sup>53</sup>

The two men were never on friendly terms again.

The controversy continued with little change in the basic position of the antagonists, but their letters became more polemical. Dyer's letter of 23 May ends with the statement: "I think that in the study of evolution we have had enough and to spare of facile theorizing. I infinitely prefer the sober method of Prof. Weldon, even if it should run counter to my own prepossessions, to the barren dialectic of Mr. Bateson."<sup>54</sup>

And Bateson's of 30 May concludes: "The facts I have been able to collect may have been few, but by a study of the writings of my antagonists, I have not been able to add materially to their number."<sup>55</sup>

The public controversy died in June of 1895 when *Nature* refused to publish anything more on the subject, but the antagonisms it generated had consequences not dreamed of by the participants. The argument over Cineraria set the stage for a continuing confrontation between Bateson and the Darwinists. Bateson knew he was bucking the tide and desperately feared his views would be forced into oblivion. He reacted vigorously against this possibility by starting breeding experiments which might reinforce his position, and by constant rebuttal of his critics.

#### THE STRUGGLE OVER THE EVOLUTION COMMITTEE

In 1895 the first report of Galton's committee was issued. It consisted of two papers by Weldon. The first, already mentioned, dealt with the correlation of death rates with certain characters of the shore crab. The second, read at the same meeting as Dyer's first Cineraria paper, was a short broadside aimed directly at Bateson's belief in the discontinuity of evolu-

53. Ibid.

54. Letter from W. T. Thiselton-Dyer, 13 May 1895, *Nature* 52 (1895): 79.

55. Letter from William Bateson, 26 May 1895, *ibid.*, p. 104.

tion. Weldon did not deny "the possible effect of occasional 'sports' in exceptional cases" but claimed that natural selection of small variations was sufficient to explain the direction and rate of evolution. He further stated that "the questions raised by the Darwinian hypothesis are purely statistical, and the statistical method is the only one at present obvious by which that hypothesis can be experimentally checked."<sup>56</sup> This was a strong statement considering the small amount of evidence Weldon had collected.

Bateson was disturbed by the report of the committee. He found that Weldon had not measured crabs in the same stage of molting. Since the magnitude of the character measured by Weldon changed after each molt, Bateson thought his results were invalid. He wrote a series of four letters to Galton, as chairman of the committee, explaining his criticism of Weldon's work. He even offered to print his letters for distribution to the members of the committee. Galton passed Bateson's criticism on to Weldon. The three then engaged in a flurry of correspondence concerning the report and the aims of the committee.<sup>57</sup>

Galton reacted to Bateson's criticisms with mixed feelings. He believed Bateson was rather pushy. And Bateson's lack of sympathy for the statistical treatment of biological problems, the express purpose of the committee, was obvious. But concerning the mechanism of evolution, Galton agreed with Bateson, not Weldon. Galton's solution to this dilemma was typically idealistic. He would add to the committee Bateson and other evolutionists whose interests were not primarily biometrical. His hope was that the enlarged committee would work to produce a broadly based view of evolution.

Pearson's belief was that Galton suggested Bateson be added to the committee because he "was so weary of Bateson's incessant letters to the committee."<sup>58</sup> But Galton really thought Bateson had much to offer the committee, a view

56. W. F. R. Weldon, "Remarks on Variation in Animals and Plants," *Proceedings of the Royal Society* 57 (1895): 380, 381.

57. BPB 10, 13, and 15. An almost complete record of the correspondence is in the Bateson Papers.

58. Pearson to Galton, 14 July 1906, in Pearson, *Galton*, 3A:290.

Weldon and Pearson did not share. In a letter dated 17 November 1896, Galton pleaded with Weldon: "It would in many ways be helpful, if Bateson were made a member of our Committee, but I know you feel that in other ways it might not be advisable. The other members besides yourself hardly do enough."<sup>59</sup>

Pearson has stated that the difference in Galton's and Weldon's views of evolution "by no means caused friction between the Chairman and Secretary of the Committee."<sup>60</sup> This cannot be entirely true, because both Weldon and Pearson were opposed to a widening of the committee to include Bateson and other nonbiometrical evolutionists, and Galton was definitely in favor of such a move. Both Pearson and Weldon sensed that a committee of diverse interests would be bogged down by controversy, instead of providing a well-rounded view of evolution as Galton hoped.

In December 1896, Pearson joined the committee. On 1 January 1897, Galton wrote Bateson: "We are going to have a Committee meeting soon. Both Weldon and myself are desirous that you should join us. Would it be agreeable to you that we should propose your name?"<sup>61</sup> Bateson replied:

I very much appreciate the suggestion that you and Weldon so kindly make, that I should join the Measurements Committee. On the whole however I think I had better not. I am not convinced that the present lines of inquiry of the Committee are fruitful and I do not think it is likely that the results will be at all proportionate to the labour expended.<sup>62</sup>

But within the month Galton convinced Bateson that the committee would change in a suitable direction. In late January, Bateson, along with F. D. Godman, Ray Lankester, Thiselton-Dyer, and five others joined the committee. At the next meeting on 11 February 1897, with the new members present, it was decided to change the name of the committee to

59. Galton to Weldon, 17 November 1896, *ibid.*, p. 127.

60. Pearson, *Galton*, 3A:126.

61. BPB 15. Weldon was not "desirous" that Bateson should join the committee. This was Galton's way of trying to make Bateson feel welcome.

62. Bateson to Galton, 3 January 1897, *ibid.*

the Evolution Committee of the Royal Society. Added to its original statement of purpose was the "accurate investigation of Variation, Heredity, Selection, and other phenomena relating to Evolution."

The fears of Weldon and Pearson were immediately realized. The new members showed little sympathy to the biometrical approach, and in some cases, much antagonism. The day after the 11 February meeting Pearson wrote to Galton:

The Committee you have got together is entirely unsuited. . . . It is far too large, contains far too many of the old biological type, and is far too unconscious of the fact that the solutions to these problems are in the first place statistical, and in the second place statistical, and only in the third place biological.<sup>63</sup>

Of course many of the new members found this attitude antagonistic and for the next three years the committee was largely disorganized.

During these three years Galton and Pearson published several papers on the law of ancestral heredity.<sup>64</sup> These papers left a trail of confusion about the meaning and application of the law.<sup>65</sup> They also contributed to Bateson's disillusionment with the biometrical approach to the problem of evolution and increased his desire to redirect the aims of the Evolution Committee.

In *Natural Inheritance* Galton had stated his law tentatively because he admittedly had insufficient evidence. At that time, 1889, he hesitated to apply it beyond the grandparental generation. But in 1897, with new data in hand on the inheritance of coat color in Basset hounds,<sup>66</sup> Galton was emboldened to state his law as follows, in what we shall term form A:

The two parents contribute between them on the average one-half, or (0.5) of the total heritage of the offspring; the

63. Pearson to Galton, 12 February 1897, in Pearson, *Galton*, 3A:128.

64. Note that Pearson did not give the law this name until 1898.

65. Much of this confusion was caused by technical considerations. What follows in the text is only a summary of these considerations. For a full exposition and support for statements made in the text, see the Appendix. The text should be read before the Appendix.

66. Galton's data came from records kept by Sir Everett Millais over a period of twenty years.

four grandparents, one-quarter, or  $(0.5)^2$ ; the eight great-grandparents, one-eighth, or  $(0.5)^3$ , and so on. Thus the sum of the ancestral contributions is expressed by the series  $(0.5) + (0.5)^2 + (0.5)^3$ , etc., which, being equal to 1, accounts for the whole heritage.<sup>67</sup>

Below on the same page Galton stated his law in another form. Supposing the deviation of the offspring from the mean  $M$  to be  $D$ , the deviation of the parents from  $M$  to be  $D_1$ , the deviation of the grandparents from  $M$  to be  $D_2$ , etc., Galton claimed his law took the form B:

$$M + D = \frac{1}{2}(M + D_1) + \frac{1}{4}(M + D_2) + \text{etc.}$$

$$= M + (\frac{1}{2}D_1 + \frac{1}{4}D_2 + \text{etc.}).$$

Galton said this form of the law showed that "the law may be applied either to total values or to deviations."

Unfortunately, the two forms in which Galton stated his law are mathematically inconsistent; yet he used them interchangeably in his calculation. This of course led to much confusion. Forms A and B caused other problems. They were statistical statements of phenotypic resemblances. But Galton claimed form B could be inferred a priori from the physiology of the hereditary process. Thus many biologists were led to believe that if they disproved Galton's conception of the physiology of heredity, a task easily accomplished after the rediscovery of Mendelian inheritance, they also disproved his law of ancestral heredity. As stated, however, forms A and B were statistical statements of phenotypic resemblances and could hold whatever the physiology of heredity might be, as Pearson continually pointed out. One further problem which added to the confusion was Galton's lack of clarity about the sort of variation to which his law applied. It applied to characters which were inherited discontinuously, such as eye color, but not to sports, which were also inherited discontinuously, or to characters involved in hybridizations. It was anything but obvious where Mendelian characters fit into this scheme, and the confusion of the Mendelians after 1900 concerning Galton's law is understandable.

67. Francis Galton, "The Average Contribution of Each Several Ancestor to the Total Heritage of the Offspring," *Proceedings of the Royal Society* 61 (1897): 402.

Galton's formulation of his law in 1897 was confusing enough, but that was just the beginning. The paper on inheritance in Basset hounds stimulated Pearson to reevaluate Galton's law. Pearson wrote a paper in which he revised Galton's law considerably, beyond anything Galton might have done on his own. Then Pearson promptly christened his new creation "Galton's Law of Ancestral Heredity."<sup>68</sup> The resulting confusion of biologists about Galton's law was to make Pearson wish he had used a different choice of words. Pearson later had to point out over and over how his own conception of the law of ancestral heredity differed from that of Galton.

Pearson's expression of the law of ancestral heredity was mathematically far more sophisticated than Galton's and in some ways bore little resemblance to Galton's. It had several extra variables, was based upon statistical correlations not upon resemblances as Galton had imagined, and no longer applied to nonblending inheritance, as in Galton's case with Basset hounds. The Basset hound data had of course supplied Galton with his only empirical "proof" of his law. Furthermore, Pearson showed that his conception of the law was completely consistent with gradual Darwinian selection, whereas Galton had repeatedly expressed the belief that regression and continuous evolution were inconsistent. Pearson concluded his 1898 paper with the following glowing statement about "Mr. Galton's Law" (as revised by Pearson):

It is highly probable that it is the simple descriptive statement which brings into a single focus all the complex lines of hereditary influence. If Darwinian evolution be natural selection combined with heredity, then the single statement which embraces the whole field of heredity must prove almost as epoch-making to the biologist as the law of gravitation to the astronomer.<sup>69</sup>

Pearson sent the paper to Galton as a New Year's greeting, 1 January 1898. Galton answered on 4 January: "You have indeed sent me a most cherished New Year greeting. It delights me beyond measure to find that you are harmonizing

68. Karl Pearson, "Mathematical Contributions to the Theory of Evolution. On the Law of Ancestral Heredity," *Proceedings of the Royal Society* 62 (1898): 386.

69. Ibid., p. 412.

what seemed disjointed, and cutting out and replacing the rotten planks of my propositions."<sup>70</sup> Thus Galton, now nearly seventy-six years old, gave his hearty approval to Pearson's revisions of his law of ancestral heredity.

The result was nearly complete confusion surrounding the meaning of the law of ancestral heredity. Not only were Galton's statements of the law mathematically inconsistent and unclear in their relationships to hereditary processes, but also Pearson's revised law, going by the name of Galton's law, was significantly different from anything Galton had previously imagined. Biologists were naturally confused about the meaning and application of Galton's law. Some believed it meant one thing, and some another. Usually they knew that Pearson had revised the law, but they could not follow his mathematics and clung to Galton's more accessible statements of it. Probably the only persons to correctly understand Pearson's revisions of Galton's law were Pearson and some of his students. The confusion surrounding Galton's law was so complete that biologists never straightened it out. The rise of population genetics showed that Galton's law was irrelevant and it simply dropped from sight.

One immediate consequence of Galton's and Pearson's papers in 1897 and 1898 was to convince Bateson, though he could not follow the mathematics, that Pearson had subverted Galton's ideas on heredity from discontinuous evolution to the cause of gradual Darwinian evolution. Moreover, Pearson had apparently captured the aging Galton's favor in this endeavor. Bateson became determined not to lose the Evolution Committee to the work of Pearson, Weldon, and Galton.

In 1897, soon after he joined the committee, Bateson was awarded a small grant which he used to begin experiments in poultry and plant breeding. He hoped to turn the interests of the committee to research of this sort. Pearson and Weldon were annoyed by the whole situation and attempted to disband the committee rather than have it fall into the hands of the opposition. In a letter dated 5 June 1899, Weldon expressed to Bateson his belief that "the Evolution Committee is a mis-

70. Pearson, *Galton*, 3B:504.

take."<sup>71</sup> On 6 November 1899, Weldon was again writing Bateson, this time to arrange a meeting in which the committee would determine its fate.<sup>72</sup> Weldon was clearly sick of the committee and hoped it would disband. Bateson wanted to save the committee as a source of publication and financial support for research on the problems of variation.

Recognizing his failure to create a viable committee, Galton resigned on 25 January 1900. Pearson and Weldon resigned at the same time hoping the Evolution Committee would collapse. But Bateson gained enough support to save it. In February 1900, the committee elected Godman as chairman and Bateson as secretary. The efforts and reports of the Evolution Committee became exclusively devoted to the work of Bateson and his followers.

Galton, Pearson, and Weldon remained close friends. But it was probably Galton's adherence to discontinuity in evolution which led to his widening of the committee against the wishes of Weldon and Pearson, and thus to an increase of hostilities between the biometricalists and Bateson's group.

Each side believed its position was under heavy attack. The biometricalists were extremely unhappy about the fate of the committee. Pearson later reported bitterly that "a definite plan was formed about 1896 to eject the biometricalists and take possession of the Evolution Committee," and that "the capture of the Committee was skilful and entirely successful."<sup>73</sup> What had appeared to be an ideal committee had been subverted to antagonistic research, and an avenue for publication of biometrical work closed. In addition to the attack from the Batesonians, the biometricalists were feeling the brunt of the resentment from the old guard Darwinists, who had little appreciation of the new statistical analysis of evolution. Bateson and his followers had consolidated a new position in the Evolution Committee but still felt that position precarious. They were determined to have their views recognized. Thus the situation was already tense at the time Mendel's work on heredity was rediscovered.

71. BPB 15.

72. Ibid.

73. Pearson, *Galton*, 3A:287, 127.

### 3 The Conflict Between Mendelians and Biometrists

MENDEL'S THEORY OF HEREDITY, REDISCOVERED IN 1900 BY HUGO de Vries, Carl Correns, and Erich von Tschermak, intensified the already heated controversy about the continuity of evolution. After 1900, when Bateson became a champion of Mendelism and Pearson named his science biometry, the controversy became known to the public as the conflict between the Mendelians and biometrists. The conflict drove a wedge between Mendel's theory of heredity and Darwin's theory of continuous evolution and consequently delayed the synthesis of these theories into population genetics.

- Bateson began breeding experiments in 1897. He had not discovered Mendelian ratios by 1900, but he was prepared to understand the results of Mendel's experiments. In 1899 he proposed experiments similar to those of Mendel:

What we first require is to know what happens when a variety is crossed with its *nearest allies*. If the result is to have scientific value, it is almost absolutely necessary that the offspring of such crossing should then be examined *statistically*. It must be recorded how many of the offspring resembled each parent and how many shewed characters intermediate between those of the parents. If the parents differ in several characters, the offspring must be examined statistically, and marshalled, as it is called, in respect of each of those characters separately.<sup>1</sup>

Mendel would have liked the proposal.

Bateson expected the results from his experiments to support the theory of discontinuous evolution. He said there were two primary problems with Darwin's idea of natural selection: the selective value of small variations was negligi-

1. William Bateson, "Hybridization and Cross Breeding as a Method of Scientific Investigation," *Journal of the Royal Horticultural Society* 24 (1900); reprinted in B. Bateson, *William Bateson*, p. 166.

ble, and the "swamping effect of intercrossing" obliterated the variation upon which selection acted. He believed that both difficulties disappeared if selection acted upon large discontinuous variations. Such variations had high selective value and were not obliterated by intercrossing.

By 1899, Bateson was prepared to understand Mendel's experiments dealing with discontinuous variations. On 8 May 1900, he was on his way to the Royal Horticultural Society to read a paper entitled "Problems of Heredity as a Subject for Horticultural Investigation." Mrs. Bateson later told the story:

He had already prepared this paper, but in the train on his way to town to deliver it, he read Mendel's actual paper on peas for the first time. As a lecturer he was always cautious, suggesting rather than affirming his own convictions. So ready was he however for the simple Mendelian law that he at once incorporated it into his lecture.<sup>2</sup>

Bateson was happy with his find. Mrs. Bateson remarked: "Mendel's work fitted in with Will's with extraordinary nicety. . . . His delight and pleasure on his first introduction to Mendel's work were greater than I can describe."<sup>3</sup>

Bateson believed that Mendelian heredity, which treated discontinuous variations and prevented swamping, was the perfect theory to complement the discontinuous theory of evolution. When published, the lecture in which he first mentioned Mendel contained the statement:

These experiments of Mendel's were carried out on a large scale, his account of them is excellent and complete, and the principles which he was able to deduce from them will certainly play a conspicuous part in all future discussions of evolutionary problems.<sup>4</sup>

Bateson's conclusion was that Mendelian inheritance supported discontinuous evolution.

Yet his was not the only possible conclusion. Mendel utilized only discontinuous characters in his experiments with peas,

2. *William Bateson*, p. 73.

3. *Ibid.*, pp. 70, 73.

4. *William Bateson*, "Problems of Heredity as a Subject for Horticultural Investigation," *Journal of the Royal Horticultural Society* 25 (1900); reprinted in B. Bateson, *William Bateson*, p. 175.

but he also described an experiment with two varieties of *Phaseolus*. One variety had white flowers and the other purple. When crossed, the hybrids all produced purple flowers. The seeds from the hybrids produced plants with flowers of a series of colors, from purple red to pale violet to white. Mendel concluded that

even these enigmatical results, however, might probably be explained by the law governing *Pisum* if we might assume that the colour of the flowers and seeds of *Ph. multiflorus* is a combination of two or more entirely independent colours, which individually act like any other constant character in the plant.<sup>5</sup>

Thus Mendel indicated that his theory might account for even a continuous array of variation. A Darwinian need not reject Mendel's theory as unsuitable for explaining continuous variation and, in turn, continuous evolution.

\* Pearson and Weldon might have argued that Mendelism supported Darwinian evolution. But Bateson made the more obvious connection between Mendelism and discontinuous evolution. In reaction the biometricians viewed Mendelism as a threat. Consequently the six years following the rediscovery of Mendelism witnessed increasingly bitter confrontations between the Mendelians and biometricians. Each confrontation is treated here as a unit, though several were often in progress at one time. The first controversy began in 1900 before Mendelism had become a heated issue.

#### THE HOMOTYPOSIS CONTROVERSY

Karl Pearson worked on his theory of homotyposis in the summer of 1899. On 6 October 1900, he submitted to the Royal Society an abstract and read it on 15 November, by which time he had completed the entire memoir.<sup>6</sup> The theory of

5. Gregor Mendel, *Experiments in Plant Hybridization* (Cambridge: Harvard University Press, 1958), p. 30. This translation of Mendel's paper was made by the Royal Horticultural Society, with footnotes and commentary by William Bateson.

6. Karl Pearson, "On the Principle of Homotyposis and Its Relation to Heredity, to the Variability of the Individual, and to That of the Race. Part I. Homotyposis in the Vegetable Kingdom," *Philosophical Transactions of the Royal Society*, A, 197 (1901): 285-379.

homotyposis was Pearson's attempt to simplify the whole problem of heredity. He argued that: (1) an individual organism produces "undifferentiated like organs," such as blood corpuscles, flower petals, tree leaves, or fish scales. Yet these organs are not exactly alike; the "undifferentiated like organs of an individual possess a certain variability, and . . . this variability is somewhat less than that of all like organs in the race";<sup>7</sup> (2) the sperm cells and ova "may each be fairly considered as 'undifferentiated like organs'";<sup>8</sup> (3) the offspring are fair representatives of the parental germs; (4) therefore the quantitative resemblance between offspring of the same parent should be the same as the quantitative resemblance between undifferentiated like organs in an individual organism.

The undifferentiated like organs Pearson called "homotypes." Homotyposis was "the principle that homotypes are correlated, i.e., that variation within the individual is less than that of the race, or that undifferentiated like organs have a certain degree of resemblance."<sup>9</sup> Pearson argued that heredity was only a special case of homotyposis. Consequently, "when we ascertain the sources of variation in the individual, then we shall have light on the problem of fraternal resemblance."<sup>10</sup> Since the production of variability in offspring was strictly analogous to the production of undifferentiated like organs in the individual, he argued further that one should theoretically expect no more variability in sexually reproducing species than in asexually reproducing species. Pearson adhered to this belief

7. *Ibid.*, p. 287.

8. *Ibid.*, p. 288.

9. *Ibid.*, p. 294. Pearson calculated the correlation between homotypes as follows. He collected a set number of leaves (or whatever character he was investigating), usually 26, from each of about 100 trees. Each leaf was individually classified or measured. Then for the leaves on each tree he took all the possible pairs, or  $\frac{1}{2}(26 \times 25) = 325$  pairs. Then he entered each pair in a correlation table using each member of the pair as the "first" leaf, rendering the table symmetrical. Thus the 325 pairs gave 650 entries in the correlation table. Repeating this procedure for the 99 other trees provided 65,000 entries in all in the table. Using the standard procedures Pearson then calculated from the table the correlation between leaves on a single tree.

10. *Ibid.*, p. 291.

for many years. But curiously, he was soon to be among the first to deduce that in sexually reproducing species the genetic recombination predicted by Mendelian heredity could provide vast numbers of genetic variants.

In the paper Pearson produced a theoretical argument, based on dubious assumptions, that fraternal correlation equalled homotypic correlation. And he presented some sixty pages of data from the vegetable kingdom. The data yielded a mean value of homotypic correlation of 0.4570. From other sources Pearson had already obtained a value of 0.4479 for fraternal correlation. Thus homotypic correlation and fraternal correlation were "sensibly equal." Pearson believed he had proved that the variation of undifferentiated like organs in an individual was the same phenomenon as variation between brothers.

If true, Pearson's homotyposis theory would have been a stunning contribution to biology. Homotyposis was perhaps comparable to the generalization "ontogeny reproduces phylogeny" of von Baer, Haeckel, and Balfour, but its biological foundations were just as weak.

Bateson attended the meeting of the Royal Society when Pearson read his abstract. Pearson reported to Galton that Bateson "came to the R.S. at the reading and said there was nothing in the paper."<sup>11</sup> Bateson had been appointed as one of the referees who would decide whether the Royal Society should publish Pearson's completed memoir, and he had prepared detailed criticisms. He even told Pearson at the meeting that he had written an unfavorable report.

When Bateson was writing his criticism of Pearson's homotyposis paper he had been acquainted with Mendel's theory of heredity for almost six months. Using Mendel's theory he could have devastated Pearson's theory. Pearson had assumed the sperm cells and ova were undifferentiated like organs. But Mendel believed his experiments showed conclusively that the germ cells must be differentiated. The translation of Mendel's paper annotated by Bateson himself states: "With *Pisum* it was shown by experiment that the hybrids form egg and pollen

11. Pearson, *Galton*, 3A:241.

### *The Homotyposis Controversy*

cells of different kinds, and that herein lies the reason of the variability of their offspring."<sup>12</sup> The offspring of the hybrids were differentiated because the germ cells were differentiated. One germ cell was different from another because it had a different combination of differentiating elements. Mendel said "we must further assume that it is only possible for the differentiating elements to liberate themselves from the enforced union when the fertilizing cells are developed."<sup>13</sup> Thus the differentiation which occurred in the development of a single plant was not differentiation of the germ plasm. That occurred only in the production of germ cells. Variation in a single plant was fundamentally different from variation in the offspring of that plant. Clearly Mendel's theory was contradictory to Pearson's homotyposis theory.

Bateson did not use the criticism from Mendel's theory because he did not believe Mendel's "differentiating elements" were material bodies. As early as 1893, Bateson had developed a "vibratory theory of heredity," which did not fit with a materialist view of heredity, and he maintained this theory with some misgivings to the end of his life. It even caused him to reject the chromosome theory of heredity.<sup>14</sup>

In his published criticism of Pearson's homotyposis paper, Bateson indicated his complete agreement with Pearson's belief "that the relationship and likeness between two brothers is an expression of the same phenomenon as the relationship and likeness between two leaves on the same tree, between the scales on a moth's wing, the petals of a flower, and between repeated parts generally."<sup>15</sup> Evidently Bateson misunderstood or rejected what Mendel had said.

Bateson's actual arguments against homotyposis were: (1)

12. Mendel, *Experiments*, p. 35.

13. Ibid., p. 36.

14. An account of the development of Bateson's thought concerning heredity may be found in William Coleman, "Bateson and Chromosomes: Conservative Thought in Science" (unpublished manuscript to appear in *Centaurus*). Coleman is at Johns Hopkins University, Department of History of Science.

15. William Bateson, "Heredity, Differentiation, and Other Conceptions of Biology: A Consideration of Professor Karl Pearson's Paper 'On the Principle of Homotyposis,'" *Proceedings of the Royal Society* 69 (1901); reprinted in Bateson, *Scientific Papers*, 1:404.

no theoretical distinction existed between differentiation and variation in a single individual or population, as Pearson assumed. Therefore Pearson's category "undifferentiated like organs" had no existence in nature; (2) Pearson ignored the importance of "specific" and "normal" variations, which were Bateson's new names for discontinuous and continuous variations. "Specific" variations were important for evolution but "normal" variations were not. Pearson did not recognize this "fact."

Without Bateson's prior approval, his criticism of Pearson's paper was distributed to the other referees before they had received Pearson's completed memoir. Pearson was greatly disturbed by this unusual procedure and communicated his unhappiness to the Royal Society and to Bateson.

The controversy surrounding Pearson's homotyposis paper precipitated an important development in the struggle between the biometricians and Mendelians. Pearson and Weldon became so disenchanted with publication procedures at the Royal Society that they decided to start a new journal. On 16 November 1900, the day after Pearson presented the abstract of his homotyposis paper, Weldon wrote to Pearson: "Do you think it would be too hopelessly expensive to start a journal of some kind?"<sup>16</sup> Pearson suggested the name *Biometrika*; he said "the 'K' was mine (K.P. not C.P.)."<sup>17</sup> In June of 1901 Cambridge University Press agreed to publish the journal and the first issue appeared in October of that year.

When Pearson objected to the procedure adopted by the Royal Society concerning Bateson's criticism, Bateson immediately withdrew his paper until Pearson's was published. He also wrote a letter of apology to Pearson, who responded with a pleasant letter commending Bateson's action. Pearson told Bateson in this letter that the new journal *Biometrika* would not "intend to be exclusive 'Nothing will be foreign to us'—so that if you do not aid us, we at least may find room to print and meet your future criticisms."<sup>18</sup>

16. Pearson, "Weldon," p. 35.

17. Pearson, *Galton*, 3A:241.

18. Pearson to Bateson, 19 February 1901, BPB 10.

Pearson decided to wait and publish his answer to Bateson's criticism of homotyposis in *Biometrika*. In the interval Bateson tried to win Pearson over to Mendelism. He knew Pearson would be a powerful ally. On 12 October 1901, he sent a translation of Mendel's paper to Pearson, who in reply expressed skepticism about the general applicability of Mendelian inheritance. In January 1902, Weldon published a criticism of Mendelian inheritance in *Biometrika*. Bateson and Pearson exchanged heated letters concerning it. Bateson now made a last attempt at reconciliation with Pearson. He truly wanted Pearson to be on the side of Mendelism:

I respect you as an honest man and perhaps the ablest and hardest worker I have met, and I am determined not to take up a quarrel with you if I can help it. . . .

There has probably been no discovery made in theoretical biology that we can remember which approaches Mendel's in magnitude, and the consequences it leads to. This is not a matter of opinion but certain. You have worked well in the same field and if through any fault of mine you were to be permanently alienated from the work that is coming, I should always regret it. With Weldon it is different. He is a naturalist. He goes in with his eyes open. Besides, as between him and me it is too late. It was a bitter grief to me when he first made it clear to me that all partnership between us was at an end. At different times, as perhaps you know, we have each tried to renew our intercourse if not friendship, but it came to nothing and it is no use trying again. There are faults of temperament on both sides. In this matter he is now committed. How far he has mistaken not only Mendel's work but the gravity of the issue cannot be long unknown.<sup>19</sup>

Pearson replied:

I think sometimes you cannot be aware that Weldon has been for many years past one of my closest and most valued friends; that I do not readily make friends, and that when I say a man is my friend I mean that I have tested the strength of his affection in the graver matters of life, and am prepared to do for him and to accept from him anything that one human being can or will do for another. I think, as I say, that you have not known this, or possibly your references to him,

19. Bateson to Pearson, 13 February 1902, *ibid.*

—only three or four, but my memory is very jealous in such matters—would have been more guarded. As to the scientific side of the present controversies, I am perfectly ready to hear both sides, and will willingly reserve space in Part III of *Biometrika* for your defence of Mendel, if you think our Journal a suitable *locus* for your paper.”<sup>20</sup>

This exchange between Bateson and Pearson illuminates the whole conflict between the Mendelians and biometricians. For it is evident that personality clashes were as important as scientific arguments in sustaining the conflict. If Weldon had adopted Mendelian inheritance, instead of opposing it, Pearson's whole attitude toward Mendelism might have been different. If Pearson, Weldon, and Bateson had worked together, population genetics might have begun in earnest fifteen years sooner than it did.

The breach between Bateson and Pearson soon became wider. In April of 1902 Pearson finally published a long reply to Bateson's criticisms of homotyposis. He attacked Bateson's loose definitions (“My own strong opinion is that biological conceptions can be accurately defined”), his lack of mathematical understanding, and especially his theory of discontinuous evolution (“Let me state once and for all that I consider Mr. Bateson's peculiar theory of evolution by discontinuous variations untenable”).<sup>21</sup> Bateson's reply was equally caustic. He and Pearson were permanently at odds.

The homotyposis controversy did not directly involve Mendelian heredity. But it did raise powerful emotions which helped polarize Mendelism and discontinuous evolution on one side, from biometry and Darwinian evolution on the other.

#### THE MUTATION THEORY

Hugo de Vries (1848–1935) turned his attention to problems of heredity in the late 1880s. His book *Intracellular Pangenesis* was published in 1889. De Vries, believing his theory of heredity was derived from Darwin's, used Darwin's term

20. Pearson to Bateson, 15 February 1902, *ibid.*

21. Karl Pearson, “On the Fundamental Conceptions of Biology,” *Biometrika* 1:324, 331.

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for the process of inheritance. Actually de Vries's conclusions challenged the foundation of Darwinian pangenesis. Darwin conceived his theory of pangenesis primarily to account for the production of heritable individual differences, the raw material upon which selection acted, and specifically allowed for the inheritance of environmentally acquired characters.

De Vries saw Darwin's theory of pangenesis as being composed of two propositions:

1. In every germ-cell . . . the individual hereditary qualities of the whole organism are represented by definite material particles. These multiply by division and are transmitted during cell-division from the mother cells to the daughter cells.
2. In addition, all the cells of the body, at different stages of development, throw off such particles; these flow into the germ-cells, and transmit to them the qualities of the organism, which they are possibly lacking.<sup>22</sup>

The first of these propositions was the basis for de Vries's theory of heredity. The second, de Vries rejected because he did not think environmentally induced variations were inherited, as Weismann had proved with mutilations in mice. But by rejecting the second part of Darwin's hypothesis, de Vries eliminated the major mechanism for the production of individual differences, the raw material for selection. It is therefore hardly surprising that de Vries's revision of Darwin's idea of pangenesis led directly to his revision of Darwin's idea of evolution.

De Vries's theory of pangenesis contained two major propositions: (1) The hereditary characters of a species were mutually independent. If, said de Vries, “the specific characters are regarded in the light of the theory of descent it soon becomes evident that they are composed of single factors more or less independent of each other.” The independence of specific characters was “verified in a striking manner by experiments in hybridization and crossing.”<sup>23</sup> (2) For each hereditary character of a species there existed in the germ cell

22. Hugo de Vries, *Intracellular Pangenesis*, trans. C. Stuart Gager (Chicago: Open Court, 1910), p. 5.

23. *Ibid.*, pp. 11, 27.

a definite material particle which determined that character. These material particles de Vries named "pangens."

It followed from these propositions that variability was of two kinds. First, the pangens might vary in their relative number: they might become more or less numerous, or change into different combinations by hybridization. Second, a pangen might, in the process of division, give rise to an altered pangen which could become active when sufficiently numerous. The first kind of variation explained Darwin's individual differences. The second explained "new characters," such as those which appeared in sports.

In 1892, three years after the publication of *Intracellular Pangenesis*, de Vries began to hybridize plants in order to trace the independent characters in subsequent generations. Between 1894 and 1899 he became convinced that the evolution of species depended primarily upon the variations caused by alteration in the pangens. The other kind of variation, which caused only individual differences, he believed unimportant for species change. By 1899 he had observed many examples of "mutations" in his stocks of *Oenothera Lamarckiana*.

In July of 1899 de Vries traveled to England for the Horticultural Society's International Conference on Hybridization, where he met Bateson. They immediately became friends, not only because they were both interested in experimental hybridization but also because they both advocated discontinuous evolution. In addition both disliked the biometricians. Bateson wrote his wife from the meeting that "de Vries is a really nice person. . . . He is an enthusiastic discontinuitarian and holds the new mathematical school in contempt—so we hit it off in admiration."<sup>24</sup> Bateson was delighted with the international acclaim de Vries received with his rediscovery of Mendelism in 1900.

De Vries had been working on his theory of discontinuous evolution for several years and in 1900 he finished the first volume of his *Mutationstheorie*. He denied that selection

24. BPB 1.

alone was effective for the creation of new species and propounded his theory of evolution by mutation, giving examples from his stocks of *Oenothera*. On 18 October 1900, de Vries sent an advance copy to Bateson along with a letter which said: "I have now the pleasure of offering you my work on the origin of species, as discontinuous as you could hope it."<sup>25</sup> De Vries fully expected an outcry from Darwinists everywhere, especially from the biometricians in England. He wanted Bateson to join with him to present a solid front. As de Vries stated it in a letter to Bateson, "there must be no discontinuity between us, not even in the use of the word."<sup>26</sup>

The biometricians were indeed annoyed by this new attack upon Darwinian evolution. Weldon prepared a critical paper which was published in *Biometrika* in April 1902. He challenged de Vries's experimental proof that selection was incapable of changing a species, thus opening the door for Darwinian evolution. As for the positive examples from the *Oenotheras*, to which de Vries devoted one half of his large volume, Weldon used only one sentence for refutation. De Vries claimed that the offspring of most of his *Oenothera* mutants regressed to a new center of regression, but Weldon said he could not "find evidence that in any one of these numerous experiments the kind of regression ascribed to the offspring of mutations has actually occurred."<sup>27</sup> Weldon's statement was nonsensical since de Vries stated that seven of his mutant *Oenotheras* bred "absolutely constant," meaning the offspring necessarily regressed to the new type. Weldon concluded his argument with the statement that when regression "is better understood than it is at present such naturalists as Professor de Vries and Mr. Bateson will abandon their attempts to distinguish between 'variations' and 'mutations.'"<sup>28</sup>

Weldon did not bother to send de Vries a copy of his criticism. When de Vries did read the criticism, he was sur-

25. BPB 15.

26. De Vries to Bateson, 25 October 1900, ibid.

27. W. F. R. Weldon, "Professor de Vries on the Origin of Species," *Biometrika* 1:373.

28. Ibid., p. 374.

prised Weldon attacked the evidence from the *Oenotheras* so feebly. Writing to Bateson about Weldon's criticism, de Vries said:

Weldon names at the end such biologists as Bateson, and de Vries, and I was glad, when reading this, to take leave from him in such good company. If you will defend me against him I will be much indebted to you.<sup>29</sup>

Bateson had duels with Weldon after this, but he was not motivated by the defense of de Vries. He did help de Vries become a foreign member of the Royal Society and even offered to supervise an English translation of the *Mutationstheorie*. But the relationship between de Vries and Bateson cooled. De Vries had rediscovered Mendel's work; yet Bateson had become the champion of Mendelism while de Vries was finding Mendelian inheritance of little importance in the evolution of species. On 30 October 1901, de Vries implored Bateson:

I prayed you last time, please don't stop at Mendel. I am now writing the second part of my book which treats of crossing, and it becomes more and more clear to me that Mendelism is an exception to the general rule of crossing. It is in no way *the* rule! It seems to hold good only in derivative cases, such as real variety-characters.<sup>30</sup>

Bateson became more impressed with the importance of Mendelian inheritance as de Vries became less so. And as de Vries became disenchanted with Mendel, Bateson became disenchanted with de Vries.

The impact of de Vries's *Mutationstheorie* upon biologists was enormous. For many reasons biologists had become disillusioned with Darwin's idea of natural selection, and de Vries presented the first experimental evidence to support another view of the mechanism of evolution. Many biologists accepted de Vries's new theory outright, and the response was generally favorable. There were, to be sure, many old-guard Darwinists who retained their ideas. But the idea of evolution

29. De Vries to Bateson, 12 May 1902, BPB 36.

30. BPB 15.

in the first decade of the twentieth century was dominated by the surge of interest in the mutational leaps of de Vries.

The effect of de Vries's mutation theory was heightened by the growing interest in Mendelian heredity, which was demonstrated so many times with discontinuous characters between 1900 and 1910. The connection between Mendel's discontinuous variations and discontinuous evolution, although not emphasized by de Vries himself, was made by many other biologists. Many of the important adherents of Mendelian heredity during these years were also adherents of discontinuous evolution.

Many scientists thought Mendelism was necessarily associated with discontinuous evolution and was therefore anti-Darwinian. Pearson and Weldon believed this, and believed it indicated that Mendelian heredity was lacking. Pearson stated:

To those who accept the biometric standpoint, that in the main evolution has not taken place by leaps, but by continuous selection of the favourable variation from the distribution of the offspring round the ancestrally fixed type, each selection modifying *pro rata* that type, there must be a manifest want in Mendelian theories of inheritance. Reproduction from this standpoint can only shake the kaleidoscope of existing alternatives; it can bring nothing new into the field. To complete a Mendelian theory we must apparently associate it for the purposes of evolution with some hypothesis of "mutations." The chief upholder of such an hypothesis has been de Vries. . . .<sup>31</sup>

Because Pearson and Weldon thought Mendelism was necessarily associated with discontinuous evolution, they opposed Mendelism vigorously.

Curiously, Bateson, in an argument for discontinuous evolution in 1904, stated that "when the unit of segregation is small, something mistakenly like continuous Evolution must surely exist."<sup>32</sup> The history of population genetics might

31. Pearson, "Weldon," p. 39.

32. William Bateson, "Presidential Address to the Zoological Section, British Association. Cambridge Meeting, 1904," in B. Bateson, *William Bateson*, p. 238.

have been accelerated had Bateson, Pearson, and Weldon taken this remark to heart.

#### INHERITANCE IN PEAS

Weldon initiated the attack upon Mendelian inheritance in the second number of *Biometrika* (January 1902) with an article entitled "Mendel's Laws of Alternative Inheritance in Peas."<sup>33</sup> He first divided inheritance into three kinds: blended, particulate (or mosaic), and alternative. Mendelian inheritance, according to Weldon, pertained only to alternative inheritance. This was not, however, the intention of Mendel, who said that his theory could account for an almost continuous array of variations. After this initial misrepresentation of Mendel's ideas, Weldon went on to attack Mendel's "law of dominance," his "law of segregation," and his neglect of ancestry.

The first general result of Mendel's work, stated Weldon, was the law of dominance. He produced examples which indicated this law was not universally true in peas, even for the characters used by Mendel, and was therefore useless. Mendel's second result was what Weldon termed the "law of segregation." This law, he claimed, was true only in very specialized cases—an accusation which was in accordance with the evidence then available to Weldon because so few experiments had been conducted and published. He concluded with the statement:

The fundamental mistake which vitiates all work based upon Mendel's method is the neglect of ancestry, and the attempt to regard the whole effect upon offspring, produced by a particular parent, as due to the existence in the parent of particular structural characters.<sup>34</sup>

Weldon did not intend for this article to start a violent controversy but it did. Bateson was incensed when he read it. He had just submitted the first report concerning Mendelian heredity to the Evolution Committee of the Royal Society and was particularly enthusiastic about Mendelism when

33. *Biometrika* 1:228-54.

34. *Ibid.*, p. 252.

Weldon's article appeared. He immediately began to prepare a detailed refutation which was published in April 1902 with translations of Mendel's papers and his own exposition of the principles of Mendelian heredity.<sup>35</sup>

The little book crackled with fiery comments. Bateson said it was "with a regret approaching to indignation that I read Professor Weldon's criticism."<sup>36</sup> He was afraid new students of heredity might discount Mendel's ideas because of Weldon's article. He also loosed a blast at the biometrical approach:

We have been told of late, more than once, that Biology must become an *exact* science. The same is my own fervent hope. But exactness is not always attainable by numerical precision: there have been students of Nature, untrained in statistical nicety, whose instinct for truth yet saved them from perverse inference, from slovenly argument, and from misuse of authorities, reiterated and grotesque.<sup>37</sup>

Bateson actually prepared two even stronger statements for his preface, but Cambridge University Press suggested they be dropped. They were, but Bateson later said he "rather liked these two bits!"<sup>38</sup>

After close study of Weldon's arguments, it was evident to him that "Professor Weldon's criticism is baseless and for the most part irrelevant, and I am strong in the conviction that the cause which will sustain damage from this debate is not that of Mendel."<sup>39</sup> He proceeded to refute Weldon's assertion that Mendelian inheritance was applicable only to alternative inheritance. He then challenged Weldon's belief that Mendel had propounded a law of dominance and made a careful attack upon every shred of evidence Weldon had utilized.

In defense of Mendel's law of segregation, Bateson expounded the "purity of the germ cells." He cited experiments which showed that extracted recessives were "identical" to

35. William Bateson, *Mendel's Principles of Heredity: A Defence* (Cambridge: Cambridge University Press, 1902).

36. *Ibid.*, p. vi.

37. *Ibid.*, p. x.

38. William Bateson to Beatrice Bateson, 28 April 1902, BPB 26.

39. Bateson, *Defence*, p. 108.

their recessive grandparents, a phenomenon which could not be explained by Pearson's law of ancestral heredity. Bateson's choice of words here was unfortunate because segregation of other factors might make the organism with the extracted recessive distinctly different from either grandparent. Weldon later insisted that Bateson believed any organism with an extracted recessive factor must be exactly like one of its ancestors. Bateson's exposition of the "purity of the germ cells" also ignored interaction effects, which he discovered only later.

The tone of Bateson's *Defence* made the biometricians unhappy. In his memoir of Weldon, Pearson stated that "Mr. Bateson's defence deeply pained Weldon, and rendered it difficult for a finely strung temperament to maintain—as it did to the end—the impersonal tone of scientific controversy."<sup>40</sup> The truth was that Weldon was scarcely less "impersonal" than Bateson, and Pearson's own personal attacks on Bateson and others were virulent.

Weldon could scarcely reply to Bateson's able defense of Mendel's ideas. Bateson, after all, was at this time perhaps the foremost expert in the world on Mendelian heredity. Instead of a reply to Bateson's criticisms, Weldon started a new attack. In his next paper, "On the Ambiguity of Mendel's Categories," published in November 1902, Weldon first stated that he could "see no reason to modify the statements"<sup>41</sup> he had earlier made about Mendelian heredity. He went on to challenge the accuracy with which a Mendelian character might be classified. Mendel had said only that when green peas are crossed with yellow the hybrid seeds were green—the shade had not been specified. Weldon gave examples, some drawn from Bateson's work, where supposed Mendelian categories were inexact and concluded that the ancestral law of inheritance might be operating.

The Mendeliants reacted to Weldon's criticism by making certain the characters they used in breeding experiments were distinct. Bateson insisted upon this. The effect of Weldon's criticism was to delay the analysis of continuously varying

40. Pearson, "Weldon," p. 42.

41. *Biometrika* 2:44.

characters in terms of Mendelian inheritance because experimenters wanted clear-cut characters.

The controversy over inheritance in peas ended, not because the antagonists were satisfied but because new controversies concerning Mendelian heredity had come to the fore.

#### HEREDITY IN MICE

In the first report to the Evolution Committee, Bateson suggested that Mendelian ratios were to be found in mice.<sup>42</sup> Before reading this report Weldon claimed in his article "Mendel's Laws of Alternative Inheritance in Peas" that inheritance in mice did not follow Mendel's laws and must be explained by the law of ancestral heredity. Bateson of course replied to this charge in his *Defence*. Weldon had unfortunately utilized the work of the German biologist Johann von Fischer, whom he quoted as an "excellent authority." Bateson showed that von Fischer's claims were outrageous and that Weldon was making no distinction between "wild type" hybrids and "wild type" pure breeds.

Weldon decided to begin breeding experiments with mice which would prove beyond a doubt that Mendelian heredity could not account for the results. He encouraged his pupil, A. D. Darbshire, to proceed with the breeding experiments. Darbshire crossed the Japanese waltzing mouse with the common albino mouse. In his first of four reports,<sup>43</sup> published in November 1902, Darbshire recorded results from the first nine crosses. The hybrids showed four different coat patterns, so Darbshire concluded that Mendel's law of dominance did not hold. Furthermore, the offspring of inbred albinos showed less white than the offspring of albinos which had appeared in litters of piebald mice. Darbshire concluded that although "on the Mendelian hypothesis the ancestry of the albinos should make no difference: we shall see that, as a matter of

42. *Reports to the Evolution Committee of the Royal Society*, Report 1, Experiments Undertaken by W. Bateson, F. R. S., and Miss E. R. Saunders (London: Harrison and Sons, 1902), p. 145.

43. A. D. Darbshire, "Note on the Results of Crossing Japanese Waltzing Mice with European Albino Races," *Biometrika* 2:101-4.

fact, it probably does."<sup>44</sup> Weldon continually used the argument that according to Mendel's hypothesis any factor would be expressed the same way no matter what the other factors in a gamete were, and Darbishire adopted this argument.

Bateson was intensely interested in the experiment and corresponded often with Darbishire. In a letter dated 3 January 1903, Darbishire wrote Bateson, "I am absolutely unbiased about Mendel and am very keen to come to an unprejudiced conclusion on it."<sup>45</sup> But Darbishire's reports showed, and he later admitted, that he was definitely prejudiced against Mendelian heredity at this time.

When the first report was published, Bateson was immediately suspicious. He wrote Darbishire, whom he found had neglected to mention that none of the hybrids were waltzers and that all had dark eyes, even though both parents had pink eyes. This, Bateson wrote Darbishire, looked like Mendelian inheritance.

Darbishire's second report appeared in February 1903. It described the hybrids from twenty pairings and the initial results of pairing hybrids with hybrids and hybrids with albinos. The first-generation hybrids were not uniformly colored, indicating to Darbishire that coat color was not subject to Mendelian inheritance: "any modification of Mendel's hypothesis involves the uniformity of the first generation." Darbishire admitted that the appearance of albinos and waltzers was so far "in possible accordance with some form of Mendelian hypothesis." He stated flatly that "the inheritance of eye color is not in accordance with Mendel's results," because pure pink-eyed parents had produced dark-eyed young.<sup>46</sup>

Bateson in response wrote a letter to *Nature* in which he suggested that the initial strains might not really be pure, although they bred true for the waltzing and albino characters, which would account for the variation of coat color in the hybrids. He also proposed a simple Mendelian interpretation

44. Ibid., p. 102.

45. BPB 27.

46. A. D. Darbishire, "Second Report on the Result of Crossing Japanese Waltzing Mice with European Albino Races," *Biometrika* 2:170, 172, 174.

of the eye color results. Weldon reacted with a letter challenging Bateson's interpretations. A series of letters between Bateson and Weldon followed, until the editor of *Nature* refused to publish anything more on the subject.

At this time Darbishire prepared his third report; Weldon, his next attack upon Bateson's Mendelism; and Bateson, an article on color heredity in rats and mice. Darbishire's third report appeared in June 1903 and began with the familiar biometrical refrain:

It is an essential part of the Mendelian hypothesis that the (so-called "extracted") recessive individual which is produced by pairing two first crosses, is in every respect similar to the original pure recessive. It forms, in fact, the foundation on which the doctrine of the purity of the germ cells rests.<sup>47</sup>

Bateson had by now denied this many times. Darbishire, surely with Weldon's encouragement, used the argument once more to show that the results with the mice were not Mendelian.

Weldon's paper, entitled "Mr. Bateson's Revisions of Mendel's Theory of Heredity,"<sup>48</sup> appeared in the same number of *Biometrika*. He argued that when a situation which did not fit Mendel's theory arose, Bateson simply revised Mendel's ideas until they fit. This meant Mendel's ideas could explain anything, and therefore nothing. In the light of later developments in genetics, Weldon's arguments were most unfortunate. He attacked Bateson's beliefs that: (1) dominance was unessential for Mendelian inheritance; (2) atavism could be explained by Mendelian inheritance; (3) sex linkage of characters exists; and (4) sex was a Mendelian factor. In the last part of the paper Weldon attacked Bateson's revisions of Mendel as applied to Darbishire's results and decided that they were an ineffective explanation of the data.

Bateson's article "The Present State of Knowledge of Colour-Heredity in Rats and Mice"<sup>49</sup> was written independently

47. A. D. Darbishire, "Third Report on Hybrids between Waltzing Mice and Albino Races," *Biometrika* 2:282.

48. *Biometrika* 2:286-98.

49. *Proceedings of the Zoological Society of London* 2 (1903); reprinted in Bateson, *Scientific Papers*, 2:76-108.

of Weldon's. He proposed Mendelian methods for the analysis of coat color in mammals. The article answered the major points raised by Weldon and Darbshire; so Bateson rested his case until Darbshire's final results were published.

Darbshire published his major results and conclusions in January 1904. He admitted now that albinism segregated in Mendelian ratios, as did eye color, and that waltzing was completely recessive. But he went on to present what he considered to be grave challenges to further Mendelian interpretation. First, albinism was not a true recessive because variable offspring appeared in the first-generation hybrids. Second, although behaving as a recessive, waltzing did not segregate in Mendelian ratios. Darbshire's argument on this point is worth quoting because he was to retract the conclusion less than three months later:

*Waltzing* occurs in only 97 out of the 555 individuals resulting from the union of hybrids. When we compare this with the number of pink-eyed individuals (131-134) or of albinos (137) we see that the proportion of waltzing individuals cannot be regarded as a possible quarter. . . . the odds against so great a deviation being rather more than 50,000 to 1. . . . The evidence that the waltzing character does not segregate in Mendelian proportions is very strong.<sup>50</sup>

Darbshire produced other data which contradicted the Mendelian interpretation—data he called "the most conclusive results which I have obtained."<sup>51</sup> He bred together hybrids which he claimed were gametically the same but with differing amounts of albino ancestry. If purebred waltzers are denoted by W, purebred albinos by A, and hybrids by H, the three crossings Darbshire made are given in figure 1. The Mendelian interpretation would be that each of these crosses would produce equal numbers of albinos, whereas Galton's law of ancestral heredity would predict that the crosses with mice of greater albino ancestry would produce greater numbers of albinos. Darbshire's data strikingly confirmed the

50. A. D. Darbshire, "On the Result of Crossing Japanese Waltzing with Albino Mice," *Biometrika* 3:20.

51. *Ibid.*, p. 23.

law of ancestral heredity. The gist of his entire paper was that the Mendelian interpretation of heredity in mice counted for little and that the law of ancestral heredity counted for much.

Bateson immediately began to correspond with Darbshire, asking critical questions about the way the data was derived and interpreted. He pointed out numerous inconsistencies between Darbshire's fourth paper and his other papers, and

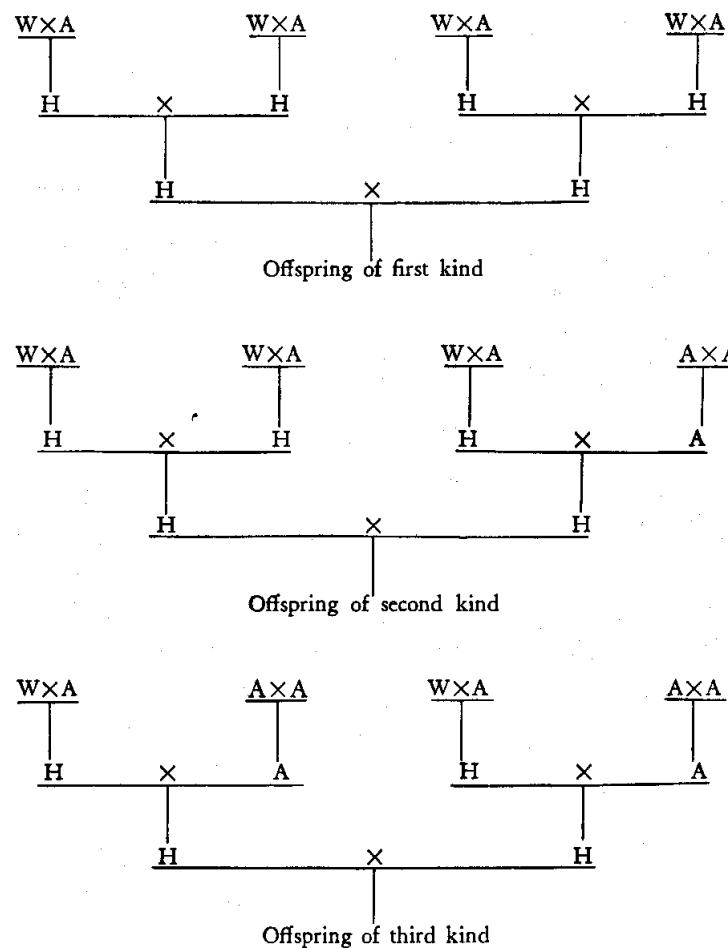


Fig. 1. Darbshire's crosses of hybrids with differing amounts of albino ancestry.

within the fourth paper itself. Soon he convinced Darbishire of two important points: that waltzers were less viable and therefore did appear in Mendelian ratios in his results, and that new pure-breeding varieties could arise discontinuously by means of Mendelian recombination. In a paper delivered 15 March 1904, Darbishire said that in the hybrid offspring ( $F_2$ ) of his experiment the Mendelian expectation was 25 percent waltzing mice: "this is very roughly what happens."<sup>52</sup> Later in the same paragraph he said "one in every four is a waltzer." To have reversed his rejection of Mendelian segregation with the waltzers was insult enough to the biometricians, but he also claimed to have produced albino waltzers. Since albinism bred pure and waltzing did too, Darbishire concluded that he had produced a new pure-breeding variety in a discontinuous leap.

Weldon and Pearson were irritated and made Darbishire aware of their unhappiness. The situation was difficult for Darbishire because he depended upon Weldon for recommendations to teaching positions. To make matters worse, Bateson now made the startling discovery that Darbishire, in his crosses of hybrids which proved that the law of ancestral heredity accounted for the phenomena better than the Mendelian hypothesis did, had not distinguished between pure-bred dominants and hybrids. The diagram of matings (fig. 1) shows why Darbishire's failure to make this distinction would lead to fewer albinos in the first and second crosses than predicted by the Mendelian hypothesis. Darbishire's most conclusive results were blatantly invalid. Moreover, Bateson's investigations now cast grave doubts about the accuracy of Darbishire's records. He revealed this to Darbishire in a letter dated 22 May 1904.<sup>53</sup> Darbishire, shaken by Bateson's discoveries, was in a very awkward position. He had already incensed Pearson and Weldon, and now Bateson was about to reveal the depths of his mistakes in his best pub-

52. A. D. Darbishire, "On the Bearing of Mendelian Principles of Heredity on Current Theories of the Origin of Species," *Manchester Memoirs* 48, no. 24 (1904): 13.

53. BPB 27.

lished scientific research. His reputation as an investigator was at stake.

He wrote Bateson a desperate letter in which he tried to arrange a secret meeting with him to put the records in order. He pleaded with Bateson not to make his discoveries public and asked for help:

I hope you will do your best to get me out of the position I am in as soon as possible and I pray you not to mention this letter to anyone. What do you suggest?

I don't mind your saying what you like about the interpretations and conclusions in the mouse paper; but to have my records discredited would be heart-breaking and render it useless and a waste of time for me to go on with the costly experiments I am carrying out now.<sup>54</sup>

Bateson replied: "It will, I think, be obvious to you on reflexion, that any communication between us which is to serve as a basis of discussion must be of a public nature."<sup>55</sup> But Bateson made no public disclosures about the inadequacies of Darbishire's work because William Castle in the United States was doing that job and because Darbishire was being scared into the hands of the Mendelians. Bateson did not wish to ruin a good thing.

At the meeting of the British Association on 18 August 1904, Darbishire stated his opinion on behalf of the Mendelians that waltzing was a recessive which segregated roughly in accordance with Mendelian expectation. Pearson was galled at this public change of view by Darbishire. On 29 September 1904, he wrote a scathing letter to *Nature* in which he reproduced Darbishire's earlier and later views side by side, with the comment:

Which writer shall a member of the inquiring general public trust? Or, if the two writers should be the same, must we assume that in Oxford, under the influence of some recessive biometer [Weldon], Mr. Darbishire failed to see that 97 in 555 was a reasonable quarter, or 20 in 555 a reasonable sixteenth, but that he has learnt in Manchester, or perhaps in

54. Darbishire to Bateson, 27 May 1904, *ibid.*

55. Bateson to Darbishire, 30 May 1904, *ibid.*

Cambridge from some dominant anaesthetist [Bateson], that these things really are so?<sup>56</sup>

Having been subjected for two years to Bateson's criticism, and now to that of the biometricians, Darbishire sought to mediate. In a paper delivered on 10 January 1905, he attempted to show that the Mendelian and biometric approaches were not contradictory.<sup>57</sup> He retracted his claim that the results of his mice breeding led necessarily to the law of ancestral heredity with the explanation that he had not chosen his hybrids properly. The biometric and Mendelian interpretations were not contradictory, he said, because each had a particular point of view. They were like skew lines which did not intersect. This paper represented a transition stage for Darbishire, who became an avowed Mendelian. In 1911 he published an influential text entitled *Breeding and the Mendelian Discovery*. In it he lamented his training in heredity as received from Weldon.

#### MENDELISM AND BIOMETRY

In his first paper on Mendel, Weldon claimed that Mendelian heredity ignored "ancestry," so the laws of Mendel and the laws of ancestral heredity of Galton and Pearson were incompatible. In his *Defence*, written in response to Weldon's paper, Bateson agreed emphatically that Mendelian heredity and the law of ancestral heredity were incompatible. He declared that "the Mendelian principle of heredity asserts a proposition absolutely at variance with all the laws of ancestral heredity, however formulated."<sup>58</sup> Weldon and Bateson attempted to show the incompatibility of the two theories of heredity because they believed that Mendelism was associated with discontinuous evolution and the laws of ancestral heredity with Darwinian evolution. This belief, a consequence of the arguments which preceded the rediscovery of Mendelism,

56. *Nature* 70 (1904): 530.

57. A. D. Darbishire, "On the Supposed Antagonism of Mendelian to Biometric Theories of Heredity," *Manchester Memoirs* 49, no. 6 (1905): 1-19.

58. Bateson, *Defence*, p. 114.

was detrimental to the synthesis of Mendelism and Darwinism.

A few were unconvinced that Mendelism and the law of ancestral heredity were incompatible. In response to Bateson's *Defence*, the British mathematician G. Udny Yule wrote a long article debunking Bateson's reasons for asserting this incompatibility. After criticizing Bateson's militant tone in the *Defence*, Yule said that the law of ancestral heredity had been applied to intraracial heredity whereas Mendelism so far had been applied to hybridization only; therefore, they could not be said to be contradictory.

Yule considered Mendel's hypothesis for explaining his results to be "ingenious and remarkable." He showed that, assuming complete dominance, the randomly bred offspring of the hybrid generation would maintain the 3:1 proportion indefinitely.<sup>59</sup> In the case of the dominant characteristic, the results predicted by Mendelian heredity were precisely the same as those predicted by the law of ancestral heredity, in the general sense that the chance of an organism with the dominant characteristic *A* producing offspring with *A* is increased if the ancestry also exhibits *A*. Yule concluded that "Mendel's Laws, so far from being in any way inconsistent with the Law of Ancestral Heredity, lead directly to a special case of that law."<sup>60</sup>

Yule knew that for a recessive trait Mendel's predictions and the law of ancestral heredity did not agree. So he asked: "In what way may the special conditions under which Mendel's Laws hold good be broadened so as to permit of a generalization of the results?"<sup>61</sup> Yule suggested that the assumption of complete dominance should be dropped and the effect of the environment upon the expression of gametic characters should be taken into account. If these two modifications were assumed, he showed mathematically that the predictions of

59. This was a special case of the Hardy-Weinberg law. Yule at this time believed the 3:1 ratio was the only stable equilibrium.

60. G. Udny Yule, "Mendel's Laws and Their Probable Relations to Intra-Racial Heredity," *New Phytologist* 1:226-27.

61. *Ibid.*, p. 227.

Mendel's theory and the law of ancestral heredity could be consistent.

Yule assailed the belief (held by Bateson, Weldon, and Pearson) that Mendelism was necessarily associated with discontinuous evolution. He suggested the multiple factor hypothesis of apparently continuous variation and the possibility that Mendelian factors might themselves be variable in small but discontinuous steps, as in the slight change of a large molecule. Since Mendelism could account for continuous variations, it was compatible with biometry and Darwinian evolution. Yule concluded with the thought that it was

essential, if progress is to be made, that biologists—statistical or otherwise—should recognise that Mendel's Laws and the Law of Ancestral Heredity are not necessarily contradictory statements, one or other of which must be mythical in character, but are perfectly consistent the one with the other and may quite well form parts of one homogeneous theory of heredity.<sup>62</sup>

Yule's excellent paper had little effect upon the widening gap between the Mendelians and biometricians. Not until R. A. Fisher's first genetical paper in 1918 was there an important attempt in England to follow the lead suggested by Yule.

Now it was Karl Pearson's turn. In 1904 he published a paper entitled "On a Generalized Theory of Alternative Inheritance, with Special Reference to Mendel's Laws."<sup>63</sup> He explored the mathematical consequences of the pure gamete theory, namely, that characters are inherited intact. He checked to see if the predictions of the pure gamete theory as defined by Mendel were in accordance with observations already made by the biometricians.

First Pearson found that (what is now called) the Hardy-Weinberg equilibrium was a necessary consequence of the pure gamete theory:

However many couplets we suppose the character under investigation to depend upon, the offspring of the hybrids—or

62. *Ibid.*, p. 236.

63. *Philosophical Transactions of the Royal Society*, A, 203 (1904): 53–86.

the segregating generation—if they breed at random *inter se*, will not segregate further, but continue to reproduce themselves in the same proportions as a stable population.<sup>64</sup>

He went on to make the extraordinary argument that sexual reproduction on the Mendelian scheme produces little novel heritable variation:

It is thus clear that the apparent want of stability in a Mendelian population, the continued segregation and ultimate disappearance of the heterozygotes, is solely a result of self-fertilization; with random cross fertilization there is no disappearance of any class whatever in the offspring of the hybrids, but each class continues to be reproduced in the same proportions. Thus our generalized theory lends no countenance to the appearance of any "mutations" within a hybrid population under random mating; the only appearance of new constitutions is in the segregating generation, or the first generation of hybrid offspring. Except at this stage, the appearance of the unfamiliar is only the chance occurrence of a very rare normal variation. When we recollect that a purely allogenic [homozygous] individual is only to be expected once in a population of  $4^m$  individuals, or if there be ten couplets, once in more than a million individuals, it will be clearly seen that the variety of some of the more exceptional normal constitutions may easily lead to their being looked upon as "mutations," even if they appear in the offspring of a population many generations removed from hybridization.<sup>65</sup>

Pearson, without realizing it, had pointed out a huge source of heritable variation as a consequence of genetic recombination. He could only see that Mendelian heredity produced no "mutations." H. Nilsson-Ehle, Edward East, and other geneticists later used Pearson's same reasoning to argue that Mendelian heredity provided most of the heritable variability in a population. Pearson was so near and yet so far from being able to harmonize his idea of Darwinian selection with his idea of Mendelian heredity. Wilhelm Johannsen used the same reasoning to argue that species change must occur by large mutational leaps, as de Vries claimed (see chap. 4).

Pearson found that the mathematical consequences of a

64. *Ibid.*, p. 60.

65. *Ibid.*

pure gamete theory were in accordance with his researches into heredity, except that the theoretical values on Mendelian assumptions, including complete dominance, for the phenotypic correlation between parent and offspring ( $\frac{1}{3}$ ), between brothers (0.3 to 0.4), and between grandparent and offspring ( $\frac{1}{6}$ ) were well below the observed values of 0.5, 0.5, and 0.2 to 0.3. Although no inherent inconsistency existed between Mendelism and the biometric description of inheritance in populations, the pure gamete theory, said Pearson, was "not elastic enough to account for the numerical values of the constants of heredity hitherto observed."<sup>66</sup>

Pearson thus rejected Mendelian heredity for the time. He did say that assortative mating or incomplete dominance would change the correlations he had derived with the pure gamete theory, but evidence was lacking about these processes. He suggested that the Mendelians produce "a few simple general principles . . . which embrace *all* the facts deducible from the hybridization experiments of the Mendelians; these can form the basis of a new mathematical investigation."<sup>67</sup> Unfortunately, it was obvious that Pearson himself would not care to undertake such an investigation.

Bateson had no way to reply to Pearson's statistical criticisms of Mendelism, but two years later Yule rebutted Pearson's calculations.<sup>68</sup> Pearson had assumed, as a "generalization" of Mendelian heredity, that only one type of homozygote determined the character upon which the correlations were calculated—which enabled him to avoid the whole question of dominance. But his claim to having avoided assumptions regarding dominance was misleading. Yule showed that Pearson's method was mathematically equivalent to the assumption of complete dominance in the correlation equations. He went on to say, as he had in 1902, that if incomplete dominance and environmental effects were taken

66. *Ibid.*, p. 86.

67. *Ibid.*

68. G. Udny Yule, "On the Theory of Inheritance of Quantitative Compound Characters on the Basis of Mendel's Laws—A Preliminary Note," in *Report of the Third International Conference on Genetics* (London: Spottiswoode, 1907), pp. 140–42.

into account, the Mendelian interpretation could account for the correlations measured in populations by Pearson and his colleagues.

Yule was ahead of his time. In 1906 he was probably the only biometrician in England who recognized not only that Mendelism and biometry were compatible but also, even more crucial, that Mendelism and Darwin's idea of continuous evolution were compatible. It is true that in 1905 and 1906, Darbishire, who had been battered by both the Mendelians and biometrists, published papers which said no conflict between Mendelism and biometry existed. But Darbishire believed they did not conflict because their points of view were so different; he did not advocate the synthesis of Mendelism and biometry, as Yule had done.

#### MEETING OF THE BRITISH ASSOCIATION, 1904

Perhaps the most heated and publicized debate between the biometrists and Mendelians occurred at the meeting of the zoology section of the British Association, 18 and 19 August 1904. Bateson, then president of the section, planned his address and organized his fellow Mendelians with the intention of scoring a crushing public victory over the biometrists. He began work on it in June and made certain his colleagues would have their best evidence prepared. Weldon boned up on all his criticisms of Mendelism in preparation for the meeting.

On the morning of 18 August, Bateson delivered his militant challenge to the biometrists. He lauded Mendelian investigations and discontinuous evolution, challenged the Darwinian selection theory, and directly confronted the biometrists. Speaking of the careful process of domestic breeding, which often utilized discontinuous variations, Bateson stated:

Operating among such phenomena the gross statistical method is a misleading instrument; and, applied to these intricate discriminations, the imposing Correlation Table into which the biometrical Procrustes fits his arrays of unanalysed

data is still no substitute for the common sieve of a trained judgment.<sup>69</sup>

The next morning the Mendelians began to present their data: Miss E. R. Saunders presented material on inheritance in plants; Darbshire presented his researches on mice with his newly acquired bias toward the Mendelian interpretation; C. C. Hurst spoke on heredity in rabbits. Then Weldon opened the discussion and raised four or five of his choice arguments against Mendelism. He concluded his remarks with the comment, as summarized by *Nature*, that

until further experiments and more careful descriptions of results were available, it was better to use the purely descriptive statements of Galton and Pearson than to invoke the cumbrous and undemonstrable gametic mechanism on which Mendel's hypothesis rested.<sup>70</sup>

The afternoon meeting promised to be lively. Punnett, speaking in 1949, recalled the action:

We adjourned for lunch and on resuming found the room packed as tight as it could hold. Even the window sills were requisitioned. For the word had gone round that there was going to be a fight. Probably other meetings were depleted—but after all the Association is British. Weldon spoke with voluminous and impassioned eloquence, beads of sweat dripping from his face, and I cannot help recalling the admiring remark made by one young Oxford man to another as they sat just in front of me, "Clever beggar that—he hasn't got to stop and think." Bateson replied and there may have been other speakers, I have forgotten. But towards the end Pearson got up and the gist of his remarks was to propose a truce to controversy for three years, after which the protagonists might meet again for further discussion. On Pearson resuming his seat, the Chairman, the Rev. T. R. Stebbing, a mild and benevolent looking little figure for a great carcinologist, rose to conclude the discussion. In a preamble he deplored the feelings that had been aroused, and assured us that as a man of peace such controversy was little to his taste. We all began fidgeting at what promised to become a tame conclusion to so spirited a meeting, especially when he came to deal

69. Bateson, "Presidential Address," in B. Bateson, *William Bateson*, p. 240.

70. *Nature* 70 (1904): 539.

with Pearson's suggestion of a truce. But we need not have been anxious, for the Rev. Mr. Stebbing had in him the makings of a first-rate impresario. "You have all heard," said he, "what Professor Pearson has suggested" (pause), and then with a sudden rise of voice, "But what I say is let them fight it out." And on that note the meeting ended. Bateson's generalship had won all along the line and thenceforth there was no danger of Mendelism being squelched out through apathy or ignorance.<sup>71</sup>

Punnett's memory was not exact: he himself spoke in the afternoon meeting, not in the morning as he recalled; also, Weldon spoke in the morning and Bateson not until afternoon. But the flavor of the victory that the Mendelians tasted that afternoon is obvious in Punnett's account, forty-five years later. As a result of this meeting Pearson attended only one more meeting of the British Association. As for Weldon, in Pearson's words, "the excitement of the meeting . . . seemed to brace Weldon to greater intellectual activity and wider plans."<sup>72</sup>

#### COAT COLOR IN HORSES

In 1900 C. C. Hurst, who had been experimenting with hybridization of orchids, became a zealous disciple of Mendelian inheritance. Hurst was, in Punnett's words, "over-apt to find the 3:1 ratio in everything he touched."<sup>73</sup> Because of his desire to give the biometricians no room for attack, Bateson was sometimes skeptical of Hurst's claims. In 1906, after a study of Weatherby's *General Stud Book of Race Horses*, Hurst came to the conclusion that chestnut was a simple Mendelian recessive to bay and brown. He wrote a short paper on the subject and asked Bateson to communicate the paper to the Royal Society, which Bateson did although with some reluctance.

Weldon was at this time chairman of the Zoological Committee, and Hurst's paper was submitted to him. He immediately "threw himself nine hours a day into the study of

71. Punnett, "Early Days of Genetics," *Heredity* 4 (1950): 7-8.

72. Pearson, "Weldon," p. 44.

73. Punnett, "Early Days of Genetics," p. 8.

*The General Studbook,"*<sup>74</sup> where he found several examples which contradicted Hurst's thesis. These exceptions he dramatically presented after Hurst had read his paper at the meeting on 7 December 1905. Hurst, standing his ground, "blandly assured Professor Weldon that he was mistaken and that these alleged exceptions were mere errors of entry."<sup>75</sup> This irritated Bateson, and he withdrew Hurst's paper from publication.

Later, Hurst discovered that Weldon's most decisive cases were indeed errors of entry. He added a note to his original paper explaining this, and Bateson resubmitted the paper.<sup>76</sup> Weldon was outraged and continued his intensive study of the *Stud Book* in order to prove that the Mendelian interpretation did not hold. The *Stud Book* was in twenty volumes, and Weldon was still working on this material when, after a sudden illness, he died on 13 April 1906.

Pearson mourned the loss of his friend. He was angry that arguing with the Mendelians had taken so much of Weldon's time. When Hurst wrote Pearson to express his regrets about Weldon, Pearson replied:

Only a few days before his death he [Weldon] condemned in stronger language than I have ever heard him use of any individual the tone and contents of the note added to your paper. It is a judgment in which I believe every man who has the interests of science at heart will concur.<sup>77</sup>

On this sour note the conflict between the Mendelians and the biometricians largely ceased. After Weldon died, Pearson redirected his interests from heredity and evolution toward the problems of practical eugenics and methods of applied statistics. He still published an occasional criticism of Mendelian interpretations, but he did not want to engage again in controversy. So in England the conflict died away.

74. Pearson, "Weldon," p. 47.

75. Punnett, "Early Days of Genetics," p. 8.

76. C. C. Hurst, "On the Inheritance of Coat Colour in Horses," *Proceedings of the Royal Society*, B, 77:388-94.

77. This quote was given by Hurst in a letter to Bateson, 9 May 1906, BPB 21.

#### THE EFFECTS OF THE CONFLICT

The conflict between the Mendelians and biometricians had its roots in the argument over whether evolution was continuous, as Darwin had claimed, or discontinuous, as Huxley and Galton had claimed. The net effect of the conflict was to exacerbate the argument over continuity in evolution. During the struggle Mendelism was firmly associated with discontinuous evolution and biometry with Darwinian evolution. De Vries's mutation theory had much appeal by itself; associated with Mendelian inheritance, it seemed even stronger, despite de Vries's own views. Thus initially, as Mendelism gained, Darwinism lost.

The conflict had a widespread influence. It touched biologists in the United States, Sweden, Germany, and France, as well as in England and Holland. The result was not always a split between Mendelism and biometry: the Americans C. B. Davenport and Raymond Pearl studied biometry in England and both became Mendelians, to the dismay of Pearson and Weldon. But the other effect of the conflict in England, the gulf between Mendelism and Darwinism, was wide in the United States as elsewhere. Pearl was a staunch believer in discontinuous evolution and Davenport leaned strongly in that direction.

Yule's approach of synthesizing Mendelism and biometry in the study of Darwinian evolution was submerged by the conflict. His was the approach of population genetics. Conflicts among his contemporaries prevented its development at this time.

In 1906 the mutation theory and Mendelism appeared to be on the way to a victory over Darwinian evolution. The opposition of the biometricians had been broken and experimental evidence was fast accumulating in favor of Mendelian inheritance. But the mutation theory claimed little positive evidence and was based upon the belief that without major mutations selection was ineffective in changing a species. This belief soon faced serious challenges.