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Evolution by Jumps: Francis Galton and William Bateson and the Mechanism of Evolutionary Change

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FRANCIS Galton (1822–1911) genuinely disagreed with his cousin Charles Darwin concerning the mechanism of evolutionary change (see Crow 1993; Maynard-Smith 1993; Gillham 2001). He felt that the small, incremental steps by which natural selection supposedly proceeded would be thwarted by a phenomenon he had discovered, which he called regression (or reversion) to the mean. Hence, Galton believed that evolution must proceed via discontinuous steps. We would call them saltations, but he named them "transiliencies." This was to some extent a throwback to views held earlier by Huxley and Lyell, from paleontological observations (see, for example, Lyons 1993, 1995). As fate would have it, Galton found himself strongly allied with the young geneticist William Bateson, who would become Mendel's great champion in Great Britain. This article describes how Galton and Bateson came independently to the conclusion that evolution must proceed in discontinuous steps.

For the first part of his career Galton's major focus was on exploration, travel writing, and geography. Under the auspices of the Royal Geographical Society he organized and led his own expedition into what is now northern Namibia, a region never before visited by Europeans. For this, he received one of the two gold medals awarded annually by the Society. He wrote a popular book on his expedition (*Tropical South Africa*, Galton 1853) and followed this with *Art of Travel* (Galton 1855), a popular guide for both amateur traveler and explorer alike, which was chock full of useful information. (The book has just been reissued.) For many years he was a highly influential member of the Royal Geographical Society. He was much involved in the organization and evaluation of the British expeditions of the 1850s and 1860s that led to the discovery of the Great Lakes of Africa and the complex drainage system that forms the source of the White Nile. Galton was also interested in meteorology and made some of the earliest weather maps of Europe and the British Isles. These were retrospective rather than prospective maps, and one such map led to his discovery of the anticyclone.

Darwin's influence was critical at several points in Galton's career. It was Darwin who convinced him to quit his medical studies and go to Cambridge to concentrate on mathematics instead. Galton's reading of *On the Origin of Species* (Darwin 1859) caused his career to change directions. He concluded, not unreasonably at the time, that it should be possible to improve humankind through selective breeding, just as it is possible to select for desirable breeds of domestic animals. "Hereditary talent and character," a two-part article in Macmillan's Magazine (1865), was Galton's first statement on the subject (Galton 1865). He obviously intended to reach a wide audience, because *Macmillan's* was one of a stable of first-rate Victorian periodicals targeted at professionals and well-educated laymen. "Hereditary talent and character" was a defining event for two reasons. First, Galton used a new technique, pedigree analysis, to examine the inheritance of "talent and character." Second, as his first biographer Karl Pearson (1924, p. 86) wrote, "Hereditary talent and character" "is really an epitome of the great bulk of Galton's work for the rest of his life; in fact all his labours on heredity, anthropometry, psychology and statistical method seem to take their roots in the ideas of this paper." Galton (1909, p. 289) concurred. Over 40 years later in his autobiography he wrote that "on re-reading these articles . . . considering the novel conditions under which they were composed . . . I am surprised at their justness and comprehensiveness."

Galton's conception of the hereditary mechanism was also derived from an idea of Darwin's, which he proposed in the second volume of a work published in 1868 entitled, *The Variation of Animals and Plants Under Domestication* (Darwin 1868). There Darwin set forth his Provisional Hypothesis of Pangenesis, a radical departure from existing "paint pot" or blending theories of heredity. The problem with such theories for Darwin was this: If a variant is likened to a few drops of black paint stirred into a bucket of white paint, the variant will vanish. Hence, Darwin hypothesized that the variants upon which natural selection acted must be particulate, and he called these particles "gemmules." To account for reversion, the occasional appearance in a pure-breeding strain of an ancestral trait, Darwin assumed the existence of dormant elements. Variations could arise by either of two mechanisms. When the reproductive organs "were injuriously affected by changed conditions," gemmules from different parts of the body might aggregate improperly so that some were in excess while others were deficient, resulting in modification and variation. Darwin's second mechanism assumed that gemmules could be modified "by direct action of changed conditions." This caused the affected part of the body to "throw off modified gemmules, which are transmitted to the offspring." Although Darwin supposed that exposure to modified environmental conditions must take place over several generations, Galton rejected the notion that variation could be acquired in this way.

Given his penchant for quantification (see Crow 1993), Galton embraced Darwin's particulate hypothesis, but then developed his own variant of pangenesis. He adopted Darwin's idea that there must be two classes of elements, which he called latent and patent. They differentiated from a common group of structureless elements in the fertilized ovum. They then followed two parallel pathways of development, first becoming embryonic elements, then adult elements, and finally converging so that a subset of patent and latent elements became the structureless elements of the next generation. A key assumption was that the patent elements of the adult could be supplemented from the latent pool, but the reverse process, while it might occur in the embryo, did not occur in the adult, making information transfer a one-way street and ruling out acquired characteristics. In succeeding papers Galton further refined his hypothesis (*e.g.*, the sum total of gemmules formed what he called the stirp, from the Latin, *stirpes*, or root—what we would call the genome).

Galton had long been interested in the properties of the normal distribution and how it could be applied to what we now recognize as continuously varying traits such as stature. He was particularly interested in understanding how such traits might be inherited, but lacking the necessary anthropometric data he turned to a model system, sweet peas, on the advice of Darwin and the botanist Joseph Hooker. He cited three reasons. Sweet peas had little tendency to cross-fertilize, they were hardy and prolific, and seed weight did not vary with humidity. His first experimental crop, planted at Kew in 1874, failed. To avoid that outcome the next year, he dispersed his sweet pea seeds widely to friends and acquaintances throughout Great Britain. The packets were lettered K, L, M, N, O, P, and Q, with K containing the heaviest seeds, L the next heaviest, and so forth down to packet Q. Elaborate instructions for planting accompanied each set.

Galton "obtained the more or less complete produce of . . . 490 carefully weighed seeds." They gave him "two data, which were all that I required in order to understand the simplest form of descent," allowing him to get "at the heart of the problem at once." By simple descent Galton meant self-fertilization. His discovery was that the "processes concerned in simple descent are those of Family Variability and Reversion." Family variability referred to the degree of variation around the mean observed among progeny seeds irrespective of whether they were large, small, or average in size. While the distribution means shifted somewhat in different sets of progeny, Galton found that the degree of variation around the mean was similar for all. By reversion Galton meant "the tendency of that ideal mean type to depart from the parent type, 'reverting' towards" the mean of the general population from which the parental seeds were selected (Table 1). He then drew a diagram plotting the diameter of the progeny seeds on the y-axis and that of the parental seeds on the x-axis, thereby constructing the first regression line (Figure 1). Initially, Galton referred to the slope of the line as the coefficient of reversion, but then changed this to regression. Later, using pedigree data from the Anthropometric Laboratory he established, initially in connection with the International Health Exhibition held in 1884, Galton was able to show that regression to the mean also applied to human stature.

Galton believed he had discovered what he referred to as a "typical law of heredity." According to this law, dispersion at one generation would be countered by reversion (regression to the mean) at the next. The alternation of dispersion and reversion would continue generation after generation "until the step by step process of dispersion has been overtaken and exactly checked by the growing antagonism of reversion." Reversion was like an elastic spring. "Its tendency to recoil increases the more it is stretched, hence equilibrium must at length ensue between reversion and family variability." Galton would interpret this as meaning that the small, incremental steps by which natural selection was supposed to proceed according to Darwin's theory simply could not work because they would be neutralized by reversion. In short, evolution had to take place in discontinuous steps that prevented reversion from occurring.

In 1888 Galton completed his two most influential scientific works. One was an article in the Proceedings of the Royal Society (Galton 1888) describing the concept of correlation, and the other was his book *Natural Inheritance* (Galton 1889). The importance of this book has long been underappreciated, particularly in view of the fact that it marks the beginning of biometrics and inspired Galton's three most significant disciples: Wil-

TABLE 1

Diameters of parent sweet pea seeds compared with the mean diameters of their progeny seeds in hundredths of an inch

Parent seed:	15	16	17	18	19	20	21
Mean diameter of progeny seed:	15.4	15.7	16.0	16.3	16.6	17.0	17.3

Adapted from F. GALTON (1889, p. 226).

liam Bateson, Karl Pearson, and W. F. R. Weldon. Pearson and Weldon took a very different message from *Natural Inheritance* from that of Bateson. Galton's chapters discussing the normal distribution and the continuous variation of characters like stature were what interested the first two scientists, but it was Galton's hypothesis of "organic stability" that intrigued Bateson. This was Galton's solution to the problem of regression to the mean, and he explained it in terms of a polygon whose many faces were uneven in length (Figure 2). If he poked the polygon gently, it might tilt toward one of the shorter sides and then rock back into its original position. It had regressed to the mean. If he pushed a little harder, it came to rest on the short face. He had created a subtype. But this process was easily reversed, going to the original side. If he flicked the polygon back on its short face once more and then jolted it sharply in a new direction, it landed on a new long side. This was a new position of stability. A "sport" had occurred that produced such a marked change that the new type created was "capable of becoming the origin of a new race with very little assistance on the part of natural selection." This sort of major discontinuous change is what we would refer to as a saltation today. In deference

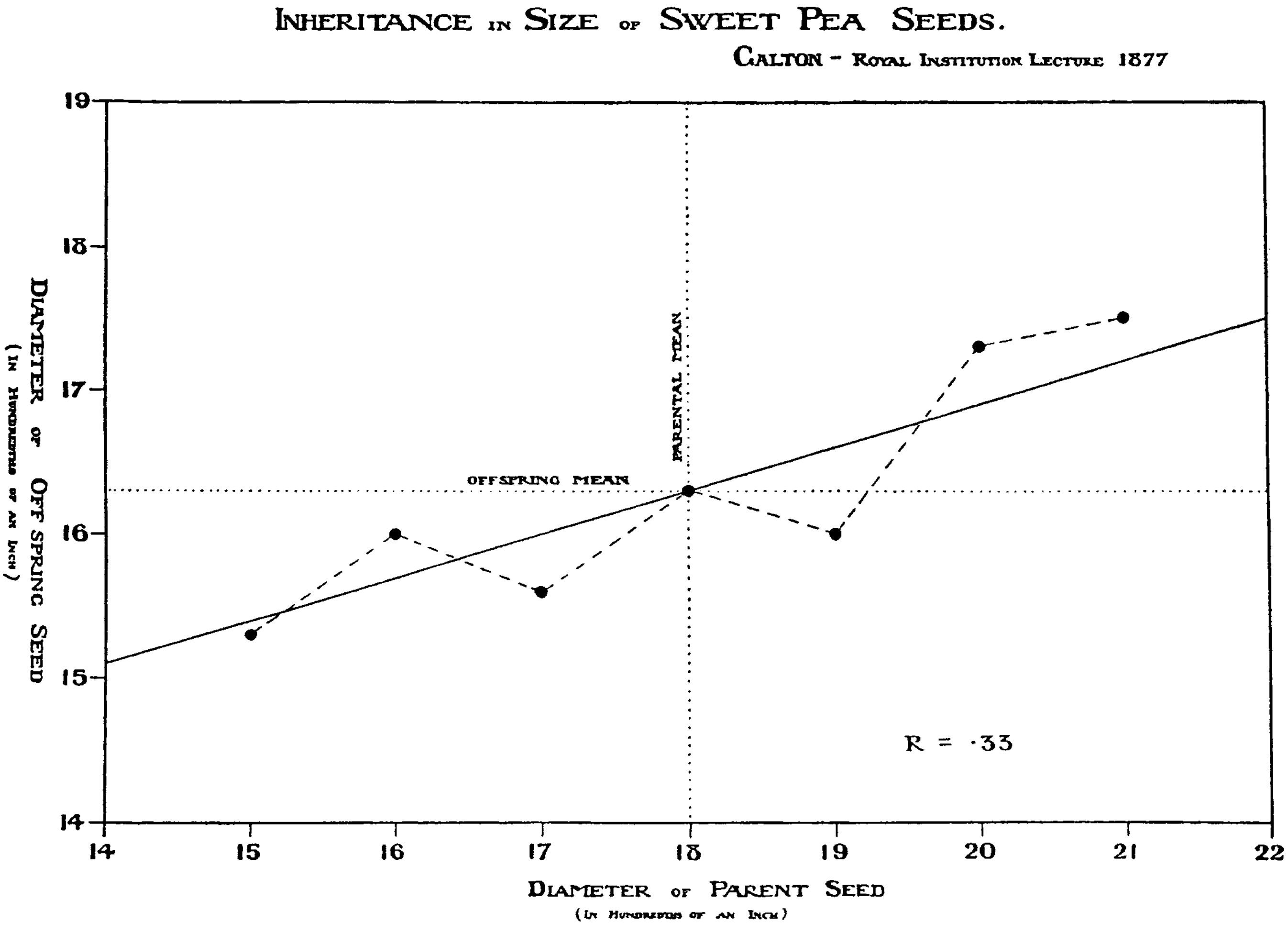

FIGURE 1.—The first regression line (from PEARSON 1930, p. 4).

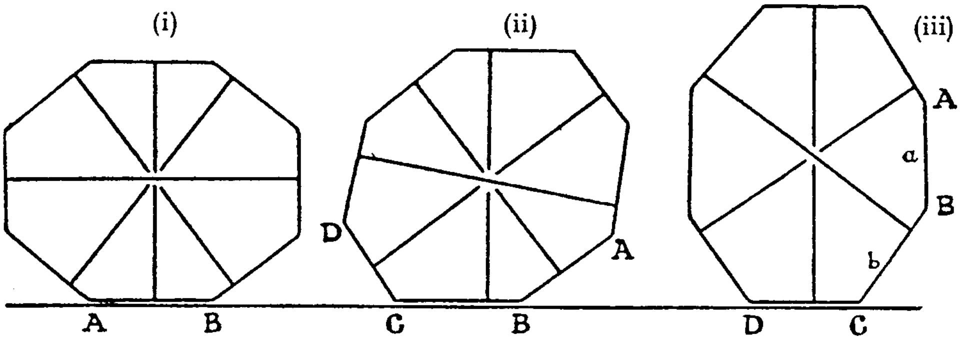

Figure 2.—Galton's use of a polygon with slightly asymmetric surfaces to illustrate his hypothesis of organic stability. In the left diagram the polygon rests on face A–B. This is a stable, symmetric configuration from which it will not budge without a forceful nudge. Such a nudge causes the polygon to come to rest on face C–B. This is an asymmetric, unstable face, and a gentle shove will bring the polygon back to rest in its original stable position on face A–B. A harder shove in the opposite direction will, however, bring the polygon to rest on face D–C. This is a stable, symmetric position once again. In short, the polygon has now achieved what Galton refers to as a "new system of stability" (from Galton 1889, p. 27).

to Darwin, Galton argued gamely that a new type could also arise "without any large single stride, but through a fortunate and rapid succession of many small ones." But he was obviously concerned about this since subtypes could revert, so there is little doubt that Galton believed such a process to be of minor importance.

Galton (1887) even tried to test his hypothesis by using a model system, the purple thorn moth (*Selenia illustraria*). To do so, he attempted the first directional selection experiment ever conducted. The moth's attraction was that it was double brooded and could be reared inexpensively in a small amount of space. In one line, long-winged males and females would be selected, while short-winged males and females would constitute the second line. Medium-winged moths would serve as a control. At each generation moths would be mounted, measured, and photographed. After six generations, selection would be relaxed, and specimens of medium wing length would be bred until all traces of long and short wings had disappeared from the lines selected for these traits. If Galton was right and selection was an unimportant force in evolution, then the long- and short-winged lines should be unstable and should quickly revert to the mean, the process being accelerated by selecting moths of medium wing length from each line. For various technical reasons the experiments failed, but their intent seems obvious.

For William Bateson, Galton's organic stability hypothesis was a case of preaching to the converted. Bateson and Weldon were close friends while at Cambridge. Both studied under the talented young morphologist Francis Balfour. Balfour encouraged Bateson to work on the hemichordate Balanoglossus, which was allied to the vertebrates and abundant in Chesapeake Bay. Weldon helped Bateson make contact with W. K. Brooks at Johns Hopkins University, who did his research at the Chesapeake Zoological Laboratory, a movable marine station established each summer between 1878 and 1906 somewhere on the shores of the vast bay. Bateson visited Brooks in 1883 and 1884 and, while Bateson learned enough about Balanoglossus to publish several papers on the creature, he took something much more important away with him. Brooks had just completed his book *The Law of Heredity: A Study of the Cause of Variation and the Origin of Living Organisms* (Brooks 1883). There he proposed a new theory of heredity designed to replace pangenesis, which permitted evolution by discontinuous change. In a key chapter, "Saltatory evolution," he cited arguments of Huxley, Galton, and Mivart in support of this mechanism. He gave examples of new races formed in sudden jumps or saltations to illustrate that "the evolution of organisms may . . . be a much more rapid process than Darwin believes."

Bateson, sold on the idea that discontinuity was the stuff of evolution, began to seek out illustrative examples. He published papers illustrating discontinuous variation in floral symmetry and in terminal forceps of earwigs and the hornlike processes seen in certain male beetles. Bateson was so excited about discontinuous variation that he "ransacked museums, libraries, and private collections; he attended every kind of 'show' mixing freely with gardeners, shepherds, and drovers, learning all they had to teach him." He put all this information together in his monograph, *Materials for the Study of Variation* (Bateson 1894). The naturalist's duty, he wrote, was to codify the facts about variation to rid biology of "the burden of contradictory assumptions by which it is now oppressed." Since variation was the essence of evolution, it was crucial to understand its nature. Although Darwin had not provided an answer, "we shall not honour Darwin's memory the less; for whatever may be the part which shall be finally assigned to Natural Selection, it will always be remembered that it was through Darwin's work that men saw for the first time that the problem is one which man may reasonably solve" (p. 1).

As Bateson saw it, the difficulty was that, while the individuals comprising a species were similar but distinct from the assemblage that constituted a related species, transitional forms were rarely found. Hence, "the forms of living things do . . . most certainly form a discontinuous rather than a continuous series." Since this was true at present, it was most likely true in the past, which meant that evolution must be the story of discontinous changes, of saltations. Since all theories of evolution started from the premise that the various forms of life were related to each other and that their diversity was the result of variation, "variation, in fact, *is* Evolution." He summed up as follows: "The first question which the Study of Variation may be expected to answer relates to the origin of that Discontinuity of which Species is the objective expression. Such Discontinuity is not in the environment; may it not, then, be in the living thing itself" (p. 17).

In the long introduction to *Materials*, Bateson referred admiringly to Galton's chapter on "Organic stability" in *Natural Inheritance*. Galton, in turn, was equally enthusiastic about *Materials* despite its intimidating size and density, 886 examples of discontinuous variation. His enthusiasm translated itself into an article entitled "Discontinuity in evolution," which he published in *Mind* (GALTON 1894). There he reviewed organic stability and considered how "the centre of a race may be changed." Once its position had been A, but later it switched to position B. How had this happened? To Galton it appeared unlikely that the switch had occurred via small steps because these intermediates merely represented extremes of two normal distributions. Their progeny would regress toward the mean in the next generation, coming to resemble more closely A or B.

Of the three explanations he cited for the differences between A and B, Galton came down strongly in favor of organic stability. No variation could "establish itself unless it be of the character of a sport, that is, by a leap from one position of organic stability to another, or as we may phrase it through '*transilient*' variation." He was "unable to conceive the possibility of evolutionary progress except by transiliencies." Galton may have used "transilient" in place of Bateson's term "discontinuous" because he felt that it actually described the evolutionary process better. A transiliency is a saltatory change, a jump or a leap, from one state to another, one race to a new race, one species to a new species. Galton noted with some irritation that he had aired these views recently "in various publications," but "seemed to have spoken to empty air." Consequently, he was delighted when he "read Mr. Bateson's work bearing the happy phrase in its title of 'discontinuous variation.'" Bateson sent Huxley a copy of his book, and Huxley approved. He replied that he was "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 to debate it."

In contrast, Weldon's review in *Nature* (WELDON 1894) was dismissive. After congratulating Bateson on his massive work and writing that he hoped Bateson would not "rest content with his already great achievement," but would "proceed with his promised second volume," he took Bateson to task. Bateson had done a nice job of assembling a multitude of facts, but his interpretation of them was seriously flawed. Weldon disputed Bateson's contention that discontinuity was not environmental, arguing that Bateson referred only to the continuity of the physical environment. However, Darwin and Wallace had argued that "the most important part of the environment against which a species has to contend consists of other living things." Furthermore, environments did not form a continuum, but over geological time were discontinuous. "These preliminary arguments in favour of Mr. Bateson's main contention therefore fail . . . when applied to any part of the process of evolution of which we know anything." It is likely that this negative review came as a complete surprise to Bateson as Weldon had been his friend. This seems a reasonable starting point for the feud that developed between Bateson and Weldon and later extended to include Weldon's friend Karl Pearson. After the rediscovery of Mendel's principles in 1900, this would turn into the famous conflict between the biometricians and the Mendelians, in which the Mendelians ultimately triumphed.

Much more important than Weldon's critique was the two-part article by Alfred Russel WALLACE (1895) in the Fortnightly Review. Since Darwin could not defend himself, having died in 1882, Wallace concluded he must do so. Wallace intended to reach a broad readership because the Fortnightly, like Macmillan's, was a top-notch Victorian periodical catering to an educated audience. The periodical, established in 1865, was, according to Anthony Trollope, one of its founders, a forum that would allow anyone "who had a thing to say and knew how to say it, speak freely. But he should always do so with the responsibility of his name attached." The Fortnightly's popular articles on science ranged widely from topics such as the nature of rainbows to medicine and meteorology. Darwin's theory of natural selection also held a prominent place in scientific discussions in the Fortnightly. In fact, George Lewes, its first editor, the writer and critic who lived happily in sin with George Eliot, had himself written a sober four-part critique of "Mr. Darwin's hypothesis" many years earlier.

WALLACE's (1895) article took both Bateson and Galton to task for their gross failure to comprehend the force of natural selection. "The effect of Darwin's work," wrote Wallace, "can only be compared to Newton's Principia. Both writers defined and clearly demonstrated a hitherto unrecognized law of nature, and both were able to apply the law to the explanation of phenomena and the solution of problems which had baffled all previous writers." But, said Wallace, a reaction had developed. Natural selection was threatened not only because Lamarck's theories were being reinstated in America and England as having equal merit, but "some influential writers" were "introducing the conception of there being definite positions of *organic stability*, quite independent of utility and therefore of natural selection." These positions were attained by discontinuous alterations. Hence, Wallace had decided he must put pen to paper, since he believed that such views were "wholly erroneous," representing "a backward step in the study of evolution." Those variations important for evolution were not necessarily "infinitesimal, or even as small as they are constantly asserted to be." Most species possessed great variability, and natural selection favored only the most fit individuals. But the struggle for existence was an intermittent affair, because there were long periods when the environment was benign, with adverse "meteorological" circumstances intervening only now and then. This view of how selection proceeds bears an eerie resemblance to the notion of a "punctuated equilibrium" as originally envisioned by ELDREDGE and GOULD (1972; see also GOULD and ELDREDGE 1993). Punctuated equilibrium was conceived as an alternative to the Darwinian explanation of why gradualism, the appearance of transitional forms between one species and another, is often not reflected by the sharp breaks found between species in the fossil record. Gradualism simply assumes that the fossil record is imperfect, and thus transitional forms are frequently absent. Punctuated equilibrium, in contrast, postulates that the fossil record is not at fault, but that there are long periods of stasis punctuated by short bursts of allopatric speciation in populations peripheral to the main species. Migration of the new species into the main area occupied by the original species and its replacement of the original species are seen as a break in the fossil record.

Wallace proceeded to show how combinations of characters led to adaptation, with examples, "and if we assume that these several characteristics are positions of 'organic stability,' acquired through accidental variation, we have to ask why several kinds of variation occurred together." Wallace wrote that Bateson's *Materials* went well beyond enumerating "interesting and little known facts" about discontinuous variation. Based on this multitude of facts, the book was actually aimed at "discrediting the views held by most Darwinians" in favor of a new theory of evolution that revolved around "sports." Darwin had rejected their evolutionary significance, but for Bateson they were central to the process. In his "Concluding reflexions," Bateson made no bones about his belief that the "existence of Discontinuity in Variation is therefore proof that the accepted hypothesis is inadequate." Wallace, incensed, quoted this statement. Then he demolished Bateson's main argument that species form a discontinuous series in a continuous environment; Bateson had failed to appreciate that even in a single locality extreme environmental variability existed, and "nothing can be more abrupt than the change often due to diversity of soil, a sharp line dividing a pine or heather-clad moor from calcareous hills." The several hundred pages of Bateson's book describing meristic variations were catalogs of "malformations or monstrosities which are entirely without any direct bearing on the problem of the 'origin of species.' " Bateson had made the egregious error of mixing malformations together with more normal variants under the heading of discontinuous variations and had faulted Darwin for ignoring them. By doing this, he had "failed to grasp the essential features which characterise at least ninety-nine per cent of existing species, which are, slight differences from their allies in size, form, proportions, or colour of the various parts or organs, with corresponding differences of function and habits" (p. 223).

Having laid waste to Bateson, Wallace wheeled the artillery around and trained his barrage on Galton. Unlike Bateson, a relatively unknown but up-and-coming scientist, Galton was a man of great scientific repute not just among his colleagues, but among the lay public as well. Wallace seized immediately upon Galton's main problem. Galton was so focused on regression to the mean that, although he admitted there was such a force as natural selection, he reasoned as if it were nonexistent. But he had missed the essential point. In Wallace's words (1895, p. 435), natural selection was a force so powerful that:

> It destroys ninety-per cent of the bad and less beneficial variations, and preserves about the one percent of those which are extremely favourable. With such an amount of selection how can there be any possible 'regression backwards towards the typical centre' when any change in the environment demands an advance in some special direction beyond it as the only means of preserving the race from extinction?

Next, Wallace gave the numerically sophisticated Galton a lesson in arithmetic. Consider an animal that lives for 10 years and produces five pairs of young each year on average. If none died within the first 5 years, there would be 6480 pairs, far too many for the environment to support. If selection were now interposed so only one breeding pair survived each year, after 10 years the original pair would be replaced by 512 pairs, still too many for the environment to support. Hence, Wallace supposed that only one-fiftieth of the progeny survived and estimated the original population would expand only 2.5-fold over 10 years, a more plausible figure.

Then Wallace took aim at Galton's organic stability hypothesis. What were these variations of Galton's that formed races and eventually new species? Did they arise independent of the environment and, if so, how did they come into harmony with the environment? Discontinuous variants were rare to begin with. Few of them had "the alleged character of 'stability,'" and they were altered only as a single part or organ. Adaptation did not involve the modification of a single character, but rather the correlated alteration of groups of characters. Even supposedly stable variants would be subjected to natural selection and would survive only if they were beneficial or at least neutral in their effect. If a new variety was among the fittest one or two percent, "it does not need this purely imaginary quality of 'organic stability' in order to survive; if it is not among this small body of the most fit . . . then . . . it will certainly not survive." Hence, "organic stability" was a meaningless concept except in the sense of adaptation to the environment in response to natural selection.

Galton was very much involved in establishing the use of fingerprinting as a method of personal identification (see STIGLER 1995). A few years earlier in 1891 he had published an important article on fingerprint classification. For some odd reason he had also engaged in a discussion of the influence of natural selection near the end of this article. He remarked that the different classes of patterns were distinguishable from each other in much the same way as different genera of plants and animals. However, natural selection was "wholly inoperative in respect to individual varieties of patterns, and unable to exercise the slightest check upon their vagaries." Using a rather peculiar line of argument, he concluded from fingerprints that "natural selection has no monopoly influence in forming genera," but that internal conditions alone were sufficient. Exactly how Galton's reasoning allowed him to make the transition from fingerprint classification in human beings, a single species, to different genera of animals and plants containing many species is obscure. However, at the end of the article, in a passage unclouded by his often confusing metaphors, Galton explained how he thought the process of evolution proceeded: "A change of type is effected, as I conceive, by a succession of sports or small changes of typical centre, each being in its turn favoured and established by natural selection to the exclusion of competitors." This is really not a bad description of the way we think natural selection proceeds, substituting mutation for sport.

Wallace ignored the latter statement and dissected Galton's earlier remarks. Galton had not only used terms vaguely, but he had compared apples and oranges. Galton's fallacious analogy between classes of similar fingerprints and genera "depends on applying the terms of classification in systematic biology to groups of single objects which have no real relation with the genera and species of the naturalist." Galton himself believed that fingerprint patterns were only slightly heritable, while heritability was the very essence of the unique features distinguishing species and genera. Wallace's logic was brilliant, his analysis impeccable, and toward the conclusion of his article he speculated as to why these two gifted scientists had been led so far astray as to the workings of the evolutionary process. He surmised that they had both looked too narrowly at "one set of factors, while overlooking others which are more general and more fundamental." He tabulated these for the edification of Bateson, Galton, or anyone else that might be marching in the wrong direction. Because they had not recognized these factors, they had "completely failed to make any real advance towards a more complete solution of the Origin of Species than has been reached by Darwin and his successors."

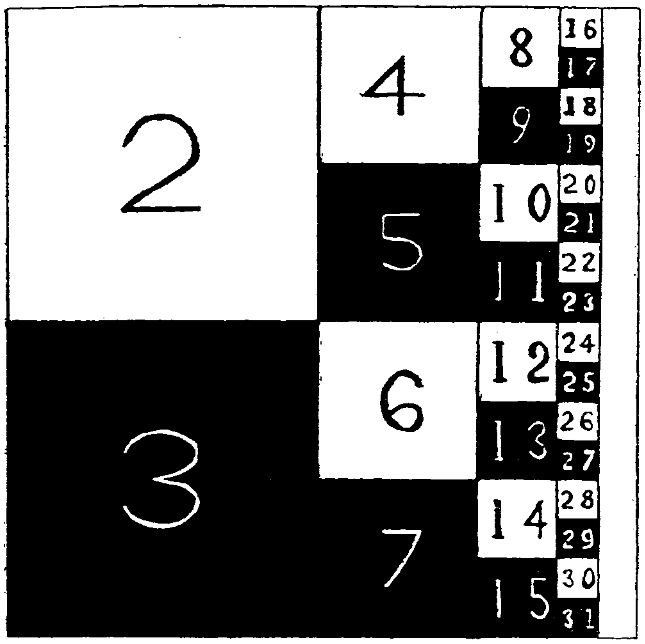

FIGURE 3.—Galton's Law of Ancestral Heredity. Male members in the pedigree are represented by even numbers in the white squares, and female members by odd numbers in the black squares. Parents (2, 3) contribute half of the heritage of their progeny, grandparents (4, 5, 6, 7) a quarter, and so forth (from GALTON 1898, p. 293).

The debate over the roles of continuous and discontinuous variation in evolution and heredity would continue to fester in the years to come, with Bateson on one side and Pearson and Weldon on the other. For Bateson the rediscovery of Mendel's principles would provide the key, but Pearson and Weldon became enamored of a different theory of heredity set forth by Galton in 1897 (GALTON 1897). His Ancestral Law of Heredity in its simplest form is easy to comprehend (Figure 3). He contemplated a continuous series with parents contributing one-half (0.5) the heritage of their offspring, grandparents one-quarter $(0.5)^2$, the eight great-grandparents one-eighth, etc. The whole series $(0.5) + (0.5)^2 + (0.5)^3 \ldots$ sums to 1, accounting for the total heritage.

Pearson was intrigued and festooned Galton's law with fancy equations (PEARSON 1898). He dedicated the paper to Galton and sent it to him as his 1898 New Year's greeting. (This seemed a nice touch, as Galton's wife Louisa had died the previous summer.) Thereafter, Pearson and Weldon would, for the most part, stress the application of Galton's law to continuously varying traits, while Bateson hammered away at one example after another of traits that showed Mendelian inheritance. The great debate between the Mendelians and the biometricians had begun. Two examples will give the flavor of the dispute. Bateson and Saunders (1902) had used the presence or absence of hairs on the leaves of Campion (Lychnis) as an example of a single pair of Mendelian alternatives. Weldon (1903) counted the number of hairs per centimeter in leaves at a similar stage of development and observed wide variations in hair numbers. Hence, Weldon viewed the absence of hairs as part of a continuum in which hair number could vary from many to zero. Similarly, in a review of Mendel's paper, Weldon (1902) chose to emphasize the variability that existed within pairs of alleles. Mendel had recognized the presence of such variability, but this was subsumed within the two alternative states posited for each character. Here is what Weldon (1903) had to say about round and wrinkled seeds: "A race with 'round smooth' seeds, for example, does not produce seeds which are exactly alike" [so] "both the category 'round and smooth' and the category 'wrinkled and irregular' include a considerable range of varieties." If seed shape was so variable, how could one be sure that only two alternatives existed?

Bateson in 1902 came surprisingly close to discovering that continuous variation could also be explained by Mendel's hypothesis. In the midst of his fight with Weldon, he wrote "The facts of heredity in the light of Mendel's discovery," a section of a Report of the Evolution Committee of the Royal Society. At one point he discussed "compound allelomorphs." He observed that for a characteristic such as stature, there must be "more than one pair of possible allelomorphs. . . . If there were even so few as, say, four or five pairs of possible allelomorphs, the various homo- and heterozygous combinations might, on seriation, give so near an approach to a continuous curve, that the purity of the elements would be unsuspected, and their detection practically impossible" (p. 60). The key distinction between Mendel's and Galton's laws of inheritance was that for "each allelomorphic pair of characters we now see that only four kinds of zygotes can exist, the pure forms of each character, and the two reciprocal heterozygotes. On Galton's view the number of kinds is indefinite." However, Galton's law might describe "particular groups of cases which are in fact Mendelian in the sense . . . that there may be purity of gametes in respect to allelomorphic characters." George Udny Yule (1902) came to a similar conclusion. He finished a paper entitled "Mendel's laws and their probable relations to intraracial heredity" by observing that if variations in the contributions of the hereditary units "take place by discrete steps only (which is unproven), discontinuous variation must merge insensibly into continuous variation simply owing to the compound nature of characters with which one deals." Neither Bateson nor Yule pursued these promising leads, and it was not until 1918 that R. A. Fisher proved that continuously varying traits could be explained by Mendel's hypothesis (Fisher 1918).

As the real artillery pieces unlimbered and began to hurl projectiles across the skies of Europe in August 1914, William Bateson was far away in Australia. He was there in his capacity as President of the British Association for the Advancement of Science to deliver addresses in Melbourne and in Sydney. His first address in Melbourne (Bateson 1914) reflected his continued skepticism that Darwin's theory proposed a satisfactory explanation for the great multiplicity of living organisms. "We have come to the conviction," wrote Bateson, "that the principle of Natural Selection cannot have been the chief factor in delimiting the species of animals and plants such as we now with fuller knowledge see them actually to be." Later he wrote that "we have done with the notion that Darwin came latterly to favour, that large differences can arise by accumulation of small differences. Such small differences are often ephemeral effects of conditions of life, and as such are not transmissible; but even small differences, when truly genetic, are factorial like larger ones, and there is not the slightest reason for supposing that they are capable of summation" (p. 638). Toward the end of his address Bateson stated (1914, p. 641) that:

> variation occurs as a definite event often producing a sensibly discontinuous result; that the succession of varieties comes to pass by the elevation and establishment of sporadic groups of individuals owing their origin to such isolated events; and that the change which we see as a nascent variation is often, perhaps always, one of loss. Modern research lends not the smallest encouragement or sanction to the view that gradual evolution occurs by transformation of masses of individuals, though that fancy has fixed itself on the popular imagination.

Although Bateson did not use the word saltation, he clearly still believed that his "large differences," the ones important in the speciation process, did not arise from the accumulation of smaller differences.

In an address to the American Association for the Advancement of Science in 1933, Richard Goldschmidt referred approvingly to Bateson's presidential address and remarked on the "evolutionary skepticism" that was driven by the early work of Bateson and others "by the results of early Mendelian work" (Goldschmidt 1933). Goldschmidt continued that he himself was not skeptical of "evolution, which I regard as a historic fact, as all biologists do," but rather "the means of evolution on the basis of genetic facts." In this regard Goldschmidt provided examples and argued "that the formation of subspecies or geographic races is not a step in the formation of species but only a method to allow the spreading of a species to different environments by forming preadaptational mutations and combinations of such, which, however, always remain within the confines of the species" (p. 547). Instead, Goldschmidt believed that rare mutations affecting the rates of important developmental processes might produce "hopeful monsters, monsters which would start a new evolutionary line if fitting into some empty environmental niche." Thus, Goldschmidt had attacked the very essence of the neo-Darwinian thesis that supposes that subspecies arise through the accumulation and selection of small genetic differences under the agency of geographic isolation, resulting ultimately in speciation. These could not, he felt, explain the origin of complex new adaptations. Goldschmidt (1940) elaborated on this theme in much more detail in his book, *The Material Basis of Evolution.* There he referred to the processes of microevolution "as used by Dobzhansky (1937) for evolutionary processes observable within the span of a human lifetime as opposed to macroevolution, on a geological scale." Goldschmidt continued that "the facts of microevolution do not suffice for an understanding of macroevolution." The term macroevolution would be used "for the evolution of the good species and higher taxonomic categories." According to Goldschmidt, "systemic mutations" fueled the process of macroevolution. It was accompanied by the repatterning of chromosomes as in the case of chromosomal rearrangements, such as inversions and translocations. Such pattern changes could have major phenotypic effects that were independent of genic changes. Another way in which macroevolution could occur was when mutations affecting early development, which "via change of rates may account for some major evolutionary changes which could not be accomplished slowly," arose. In this regard, he discussed the homeotic (a term coined by Bateson) mutants of Drosophila to illustrate how a mutation affecting segmentation in early development could lead to the appearance "of a homologous appendage in a segment to which it does not belong." Goldschmidt's point was that one or a few "genetic steps" that were small in the genetic sense, but large in the morphogenetic sense, "demonstrate that it is possible, and even probable, that macroevolution takes place without accumulation of micromutations under the pressure of selection." Later he returned once more to the notion of the "hopeful monster." These hopeful monsters were monstrosities produced by mutations that "may have played a considerable role in macroevolution."

Although Goldschmidt was recognized for his important contributions to evolutionary genetics, notably his work on geographic races of the gypsy moth (*Lymantria dispar*), prominent geneticists like Theodosius Dobzhansky (*e.g.*, in *Genetics and the Origin of Species*, Dobzhansky 1951) dismissed his macroevolutionary theory, writing that since "mutants appear in populations at first as heterozygotes, inviable and sterile heterozygotes are eliminated, regardless of how well adapted might be the corresponding homozygotes. This consideration is fatal to Goldschmidt's (1940) theory of evolution by 'systemic' mutations. Even if the inviability or sterility of heterozygotes be supposed to be incomplete, these heterozygotes will be discriminated against by natural selection" (p. 203). But the systematist Ernst Mayr was so seriously concerned over Goldschmidt's attack on the polytypic species concept that he felt it "necessary to present" additional proof in favor of geographic speciation in his highly influential book, *Systematics and the Origin of Species* (Mayr 1949).

In his book *Animal Species and Evolution*, Mayr briefly reviewed and dismissed claims of saltational evolution made by scientists like Bateson, De Vries, and Goldschmidt (Mayr 1963). He included a quote from Bateson's book, *Materials for the Study of Variation*, in which Bateson says he was convinced that continuous and discontinuous variation "are distinct essentially . . . that they are manifestations of distinct processes." Both Galton and Goldschmidt would have agreed—Galton because regression to the mean would have thwarted evolution by small, continuous steps and Goldschmidt because only macroevolution through saltational changes could lead to new species formation.

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