The Biometric Defense of Darwinism

B. J. NORTON

Department of the History and Philosophy of Science
University of Pittsburgh

INTRODUCTION

In the closing decade of the nineteenth century the study of evolution was marked by investigations of selective death rates in nature and by discussions about the types of variation that were evolutionarily significant. In one such discussion the biometricians W. F. R. Weldon (1860–1906) and Karl Pearson (1857–1936), with their investigations of death rates in nature and their laws of ancestral heredity, attempted to uphold Darwin's view that the smallest-seeming variations could be evolutionarily crucial, whereas Francis Galton (1822–1911) and William Bateson (1861–1926) argued that evolution was essentially discontinuous and due to the sudden appearance of markedly variant individuals able to transmit their novelty to subsequent generations.

THE LOGIC OF DARWINISM

If we are properly to comprehend the intellectual background and historical significance of this discussion, then we must first appreciate the logical construction of Darwin's theory of evolution by natural selection.

The keys to this are Darwin's views on heredity and variation which may be crudely summarized as follows. Darwin believed that almost any character might be inherited, and also that the usual outcome of crossing was a blend of parental characters. However, he also held that siblings were not identical, but showed variations—i.e., divergences from the parental average, and thereby from the species norm too. He held that the different types of variation formed a continuous series. At one end of this series were the small "individual differences" which made the members of a species distinguishable, and at the other were the infrequent "single variations" which could

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be sufficiently marked to brand their bearers as "sports," or monstrosities. Between these two extremes all degrees of departure from the average specific form were to be found, and Darwin implied that the more extreme the degree, the less frequent it was. All types of variation could be inherited.

For Darwin, individual differences were the building blocks of evolutionary change, and were characterized primarily by their not striking the observer as rendering their bearer markedly different from the bulk of species members. Into this category he appears to have included variations in the size, shape and color of organs, and also variation in the numbers of their repeated parts. Overall, Darwin's categorization was phenotypic and vague, but it is certainly clear that the types of normally distributed variation that Galton, Weldon, and Pearson were later to study (e.g., variation in height among the members of a population) entered his class of individual differences.

The theory of evolution by natural selection arose from the observation that, in nature, rates of reproduction were so high that anything approaching population stability could be maintained only by the operation of a high mortality rate among offspring. This overproduction implied that there was "in every case a struggle for existence, either one individual with another of the same species, or with the individuals of a different species, or with the physical conditions of life." It was probable that "variations useful in some way to each being in the great and complex battle for life should occur in the course of many generations," and it was virtually indubitable that "individuals having any advantage, however slight, over others would have the best chance of surviving and procreating their kind." This preservation of favorable variations and the allied destruction of injurious ones, Darwin called "Natural Selection" or the "Survival of the Fittest." [1]

Because variation was inherited, it followed that the next generation, composed disproportionately of the offspring of parents bearing "useful" variations, would differ from the one that preceded it. At successive reproductions new variations would be formed and would enter into the competition for survival and transmission. The net effect would be that, over a period of time, a considerable degree of change would be produced, yielding the emergence of a new species.

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[1] Charles Darwin, *The Origin of Species, a Variorum Text*, ed. Morse Peckham (Philadelphia, 1959), p. 164, sentence 13.

When first formulating his theory, Darwin had inclined to the view that it was the marked and rare single variations that were evolutionary significant.[2] New species, he had conjectured, would be formed by the accumulation by natural selection of these infrequent variations. But later, noting that such variations often lacked adaptive qualities, and seeing that, given random mating, they would soon be "swamped" by crossing with the more common normal forms, he turned increasingly to the view that new species were formed by the accumulation, by natural selection, of a much greater number of individual differences. In this latter view, the unit of evolutionary change was the whole population. These populations would present numerous individual differences for natural selection to operate upon, would be kept uniform by the intercrossing of their members, and would show a slow and intermittent but never discontinuous change, which, said Darwin, "accords perfectly well with what geology tells us of the rate and manner at which the inhabitants of this world have changed." [3]

The rejection of all forms of saltative variation was completed in the fifth edition of the *Origin of Species* (1869), where Darwin showed the extent to which he had moved toward a view of evolution as due to the natural selection of the individual differences borne by the members of an intercrossing population, by introducing the example of a bird which would be able to procure its food more easily if, counterfactually, it were to have a curved beak. If a single discontinuous variant were born having a very strongly curved beak, then it would flourish, but "there would be a very poor chance of this one individual perpetuating its kind to the exclusion of the common form." On the other hand, the formation of a whole race of birds with curved beaks would follow from "the preservation during many generations of a large number of individuals with more or less strongly curved beaks, and from the destruction of a still larger number with the straightest beaks." [4]

It is noteworthy that Darwin's dismissal of saltative variation depended only partly on his acceptance of a blending theory of inheritance, with its consequent swamping of rare variations. For he felt strongly that each species was beautifully suited to

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[2] C. Darwin and A. R. Wallace, *Evolution by Natural Selection* (Cambridge, 1958). See the "Sketch of 1842."

[3] Darwin, *The Origin of Species*, p. 202, sentence 227.

[4] Ibid., p. 178, sentence 95.11.e.

its environment and that this snugness of fit was comprehensible on the supposition that species had been produced by the accumulation, by natural selection, of innumerable small variations, "each good for the original possessor," but that it would be incomprehensible if it were supposed that new species were produced by the addition of a smaller number of very marked single variations. The advocate of evolutionary discontinuity was censured with the point that

> He will further be compelled to believe that many structures beautifully adapted to all the other parts of the same creature and to the surrounding conditions, have been suddenly produced: and of such complex and wonderful co-adaptations, he will not be able to assign a shadow of explanation . . . To admit all this is, as it seems to me, to enter into the realms of miracle, and to leave those of science.[5]

With these points in mind, it is worth remembering that Darwin's class of individual differences appears to have included all those variations which observers would agree to call slight. Let us take the hypothetical example of a mammal having a nonprehensile tail which is never used as an aid to climbing. Then, for Darwin, both variations in the length of the tail—which we might suppose to be normally distributed about some population mean—and the appearance of an individual showing a slight tendency to use its tail as an aid while climbing—which might be regarded as a first step in the evolution of a prehensile tail—would be looked upon as examples of individual differences.

The problem which Darwin did not discuss fully was that of whether or not small variations, other than in the weight or length of organs, which introduced some novelty into the situation (as in the case of the mammal which used its tail) were sufficiently common for his evolutionary scheme with its emphasis on population-uniformity maintained by a blending heredity[6] to be a credible explanation of the origin of species.

In summary, then, Darwin's theory had two interlocking parts. The first said that all modern species had been derived

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[5] Ibid., p. 267, sentence 382.65.0.50.369.

[6] Darwin's changes of view on the matter of which forms of variation were evolutionarily significant and his reactions to his critics are well dealt with in Peter Vorzimmer, "Charles Darwin and Blending Inheritance," *Isis, 54* (1963), 371–390.

from a smaller number of ancient species in a process of descent with modification. The second said that all modifications in descent, or nearly all (for Darwin recognized evolutionary mechanisms other than natural selection), were produced in a particular way: that is, by the natural selection of innumerable slight, advantageous variations.

Darwin believed that ancient forms had given rise to modern ones in a process of slow and never discontinuous modification of whole populations, each kept uniform by the intercrossing of its members. He held, in effect, that, *as a matter of historical fact, death rates in nature had on occasions been selective in respect of different types of individual difference;* e.g., in respect of longer or shorter legs. And also that *most population changes from generation to generation were explicable by the laws of heredity and variation*[7] *taken in conjunction with "initial condition" statements which described these selective death rates.*

Clearly, then, the theory included the following two assertions: (1) that, in nature, death rates were often selective in respect of the different types of individual differences manifested by the members of populations; (2) that "single variations" were evolutionary inconsequential. Therefore, to demonstrate in some particular and unesoteric case that different types of individual differences did significantly affect their bearers' chances of surviving to reproduce would lend support to Darwin's view. But, either to show on the basis of a theory of heredity that individual differences could not play a significant evolutionary role, or to demonstrate that in certain cases "single variations" had been the cause of evolutionary change, would be to exhibit the need for reformulation of Darwin's theory.

By 1892, the year in which Galton published the second edition of his *Hereditary Genius*,[8] considerable opposition had developed to the idea that evolutionary advance was due primarily to the natural selection of individual differences. Fleeming-Jenkin, in 1867 (among other criticisms of Darwin's ideas), had argued that, as a matter of observable fact, there were rapidly discovered upper limits to the degree of change which could be produced by the selection of individual differences —because it appeared that increasingly "improved" forms were

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[7] Not explicable in the sense of being *strictly* predictable, for one of the central points about variation seemed to be that one could not tell in advance what new features might be produced.

[8] Francis Galton, *Hereditary Genius*, 2nd. ed. (London, 1892).

increasingly likely to produce only offspring which varied in the direction of less rather than more "improvement."

> Although many domestic animals and plants are highly variable there appears to be a limit to their variation in any one direction. This limit is shown by the fact that new points are at first rapidly gained, but afterwards more slowly, while finally no further perceptible change can be effected.[9]

Hugo DeVries, in his 1889 work *Intracellular Pangenesis,*[10] had formulated his distinction between variation due to changes in the number of pangens of a particular type ("fluctuating variability," which included normally distributed variations) and variation due to the sudden creation of a new type of pangen ("mutation"). The latter, he wrote, was the only type of variation which could produce true evolutionary change, because it was the only form of variation whose continuation was independent of the nutritional conditions of life. Francis Galton, using his "quantum" notion of alternative positions of stability[11] (i.e., the notion that only certain forms were inherently stable, and the intermediate forms—such as might be produced by the selection of normally distributed variations —would, in a few generations, revert to one stable position or another) and misinterpreting his own discoveries in regression (see below), had argued that evolution could occur only through the emergence of "sports." [12]

However, before the appearance of Weldon's report to the Evolution Committee of the Royal Society in 1895, there were, so far as I have been able to ascertain, no published attempts to defend Darwin's thesis by demonstrating that, in nature, different grades of individual differences did materially affect their bearers' chances of surviving to reproduce.

It seems odd that the study of death rates should have to

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[9] Fleeming-Jenkin, "The Origin of Species," *North British Review, 46,* (1867), 285. Jenkin also criticized the notion of evolution having been brought about by the emergence of "sports." For, believing in a blending theory of heredity, he was able to argue that any novelty of feature would soon be "swamped" by crossing with normal forms.

[10] Hugo De Vries, *Intracellulare Pangenesis* (Jena, 1889), trans. C. S. Gager as *Intracellular Pangenesis* (Chicago, 1910).

[11] Francis Galton, *Natural Inheritance* (London, 1889), pp. 18–34. Galton's presentation of these ideas is discussed in J. S. Wilkie, "Galton's Contribution to the Theory of Evolution, with Special Reference to His Use of Models and Metaphors," *Annals of Science, 11* (1955), 194–205.

[12] Galton, *Hereditary Genius,* "Prefatory Chapter to the Edition of 1892."

await the 1890's and the coming of Weldon. Why, one is forced to ask, did attempts to confirm one of Darwin's leading hypotheses have to wait until nearly 40 years after the publication of the *Origin*? Apart from the effect of the publication of Bateson's *Materials for the Study of Variation* in 1894,[13] which argued that the natural selection of individual differences could not account for specific differences and which offered a detailed catalogue of examples of naturally occurring discontinuous variations, there appear to have been at least three reasons for this delay. First, there is the biological spirit of the times which (in England, at any rate) was not encouraging to Weldon's and Bateson's type of work. G. S. Carter, in his *A Hundred Years of Evolution*,[14] shows that, particularly in the case of zoology, the dominating academic interest of the later nineteenth century was with phylogenetic morphology. This he explains in terms of a long-standing morphological tradition in England and a *natur-philosophie* tradition in Germany. Secondly, there is the matter of methodology (see n. 53). In a period in which biologists were not noted for methodological awareness, Weldon consciously promoted a phenomenalistic philosophy of science. This stimulated him to seek out the observational content of Darwin's claims and to put these claims to empirical test. Thirdly, there is the matter of technical difficulty. To show that different grades of individual differences were associated with differing chances of surviving to reproduce was an extremely difficult matter, both technically and mathematically. Weldon was in a favorable position to overcome these difficulties. He was not only clever and hardworking, but had also read and understood the mathematics used by Galton (who had trained as a mathematician)[15] in his 1889 anthropometric work *Natural Inheritance*, and when he

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[13] William Bateson, *Materials for the Study of Variation, Treated with Especial Regard to Discontinuity in* The Origin of Species (London, 1894).

[14] G. S. Carter, *A Hundred Years of Evolution* (London, 1958), pp. 78–92. Quoting from B. Bateson, *William Bateson F.R.S.* (Cambridge, 1928), p. 42, Carter illustrates his point by showing that Bateson found it difficult to obtain permanent employment because he had gone "too far afield" from morphological work. Weldon, before moving to London in 1891, had been a Cambridge lecturer in invertebrate morphology.

[15] See F. Galton, *Memories of My Life* (London, 1909), chap. 5. Weldon's first paper on selection incorporated ideas rather similar to those contained in the section on "Natural Selection" in Galton's *Natural Inheritance*, pp. 119–124. It should be noted that Galton's primary interest was with anthropology, not with biology, and that he always operated as a private citizen, never as the holder of an academic post.

subsequently applied Galton's techniques to purely biological problems he became a skilled statistician, striking up useful and inspiring friendships with Galton and with Karl Pearson, mathematician at University College London.[16]

FIRST DEVELOPMENTS

The first mathematical studies of individual differences were carried out by Francis Galton, who, as a prelude to eugenic propagandizing, attempted to find laws which governed the inheritance of such normally distributed variations as the deviations in human height from the mean height of a race. Galton believed that whatever could be shown for stature would hold also for intelligence.

He found that, in respect of stature, sons regressed linearly on their fathers with a regression coefficient of ⅓—i.e., he found that for all fathers whose deviation (from the paternal mean) was x ins., the mean corresponding filial deviate (from the filial mean) was $\frac{1}{3}x$ ins.[17] And he interpreted this regression as being not simply to the filial mean (which in the case he studied was the same as the paternal mean), but to a *constant racial mean*[18] or, as Pearson was later to put it, a constant focus of regression. At the same time however, Galton also derived (invalidly)[19] a law of ancestral heredity[20] which had the following paradoxical quality. As first derived, the law stated that the most probable value of a child's deviate was equal to the sum of half the deviate of his mid-parent (an imaginary individual having, for example, a height equal to half the sum of the paternal and adjusted maternal heights) plus a quarter of the deviate of his mid-grandparent, plus an eighth of the deviate of his mid great-grandparent, and so on.

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[16] Karl Pearson, "Walter Frank Raphael Weldon 1860–1906," *Biometrika* 5 (1906), 1–52, esp. pp. 17–19. This memoir is the only biography of Weldon. Pearson explains Weldon's adoption of biometric methods as partly due to the fact that, shortly before reading *Natural Inheritance,* he was working on morphological problems involving the idea of correlation.

[17] Galton, *Natural Inheritance,* pp. 95–100.

[18] F. Galton, letter to *Nature,* 55 (1897), 605.

[19] The invalidity is compound. Galton wrongly assumed that regression coefficients could be multiplied together, a false assumption discussed in Karl Pearson, *The Life, Letters and Labours of Francis Galton* (Cambridge, 1914–1930), pp. iiia, 23–24. But, after this, his reasoning is invalid. This, and the relation between his statistical and physiological theories of heredity, are clearly discussed in R. G. Swinburne, "Galton's Law—Formulation and Development," *Annals of Science,* 21 (1965), 15–31.

[20] Galton, *Natural Inheritance,* pp. 134–137.

But, as applied by Galton, the law was interpreted as dealing exclusively with discontinuous attributes. For example, he was able to show that the composition of litters of basset hounds[21] (dogs which, as regards coat color, always fall into one or the other of two distinct classes, namely "tricolor" and "lemon and white") could be reasonably accurately predicted by assuming that a quarter of the puppies would take after the mother, a quarter after the father, than an eighth would resemble each grandparent, a sixteenth each great grandparent, and so on.

Failing to appreciate the consequences of the application of his law of ancestral heredity to continuous variation, Galton was able to offer some scientific support for the proposition that evolution proceeded by the sudden emergence of markedly variant individuals—"sports"—whose offspring regressed not to the old racial mean, but to a new focus of regression defined by the variant parent. In other words, these sports would act as new racial centers.[22] In extreme cases they were the founder members of new varieties, produced all of a sudden, without benefit of the aeon-consuming gradual accumulation of individual differences posited by Darwin. Galton gave little by way of example of such sports, feeling perhaps that their existence was theoretically necessary.

The support for Galton's thesis lay in his observation that the coefficients for the regression of son on parent and for the regression of son on mid-parent (call the latter b) were both less than unity. It followed, he argued, that if a living form were to be so improved by natural selection that it came to have say, a height which deviated from the original racial mean height by z ins., *then this improvement could not be maintained independently of continued selection.*For, if selec-

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[21] F. Galton, "The Average Contribution of Each Several Ancestor to the Total Heritage of the Offspring," *Proc. Roy. Soc.*, *61* (1897), 401–413. Why Galton felt able to apply his law to discontinuous attributes when he had "derived" it from data for stature is a puzzling matter. Swinburne concluded that Galton's law was in fact derived from his physiological theory (see e.g., *Natural Inheritance,* 7–14, 192–198) and was "merely tested later against the painfully accumulated data." This supposition would certainly explain Galton's amazing extrapolation if we further assumed that he regarded discontinuous attributes as controlled by the development of a single hereditary particle (or linked group), and continuously varying dimensions as controlled by a large number of independent particles, with the individual particles following the same inheritance pattern in each case.

[22] Galton, *Hereditary Genius*, p. xvii.

tion were to be completely relaxed, and inbreeding commenced, then successive generations of posterity would show mean deviates of $(b^i)z$ ins., where i is the number of reproductions which have occurred since the relaxation of selection.[23] Since b was less than one, argued Galton, it followed that the effect of the selection of extreme values of individual differences could never become independent of continued selection. This result would follow only from the spontaneous emergence of a sport.

However, as Pearson was able to show in 1895[24] and in 1898,[25] Galton's argument could hold true only if the coefficients for the correlation of a child with its father, its grandfather, its great grandfather, and so on, ran as r, r^2, r^3, etc. If they did so, then it followed that the law of ancestral heredity was false. But, if these correlations ran as 0.3, 0.15, 0.075, etc., figures which approximated quite well to the values found by Pearson in his investigations of the inheritance of stature, then the law of ancestral heredity, as stated in its application to continuously varying characters, would be correct.[26] This law, wrote Pearson, pointing out consequences which Galton had not noticed, implied that after the relaxation of selection and the commencement of inbreeding, there would be no further regression after the first reproduction.[27] Hence it transpired that, at least among those biologists who understood the multinormal probability distribution that underlay Pearson's work (a small group that included Weldon, but not Bateson), Galton's arguments for the necessity of discontinuous evolution were correctly evaluated as being invalid.

It is one of the curiosities of the history of science that, while Galton's views were often employed to support the notion that evolution occurred in a series of discontinuous jumps—see, e.g., the works of Bateson and De Vries[28]—his statistical techniques inspired W. F. R. Weldon (Professor of Zoology at University College London) and Karl Pearson (Professor of

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[23] Galton, letter to *Nature*, 1897.

[24] Karl Pearson, "Regression, Heredity and Panmixia," *Phil. Trans. Roy. Soc.*, *197A* (1896), 253–318.

[25] Karl Pearson, "Mathematical Contributions to the Theory of Evolution. On the Law of Ancestral Heredity," *Proc. Roy. Soc.*, 62 (1898), 386–412. For a detailed account of Pearson's work see my 1970 M.Phil. thesis, *Theories of Evolution of the Biometric School* (University of London).

[26] Ibid., p. 396.

[27] Ibid., p. 401.

[28] Hugo De Vries, *The Mutation Theory* (Chicago, 1910), pp. i, 104.

Applied Mathematics) with the idea of creating a new, mathematically based, and positivistically orientated evolutionary biology. These men, with their helpers, became known as the biometricians, and, seeing themselves as Darwin's true scientific heirs, adopted his doctrine of evolutionary continuity due to the natural selection of innumerable individual differences, each good for the original possessor. The flavor of their approach is well transmitted by the following statement of problems made by Weldon in 1893 and later described by Pearson as having "formulated the fundamental principles of biometry."[29]

> 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 of 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.[30]

Insofar as the biometricians divided their labor, Pearson devoted himself to formulating theories of heredity, whereas Weldon, by undertaking investigations of death rates in nature, attempted to demonstrate that evolution really did proceed in the manner Darwin had suggested, namely, by the natural selection of innumerable small individual differences.

THE IDEAS OF WILLIAM BATESON

To understand Weldon's work it is necessary to appreciate his intellectual orientation. It seems probable, although no readily available documents testify to this directly, that he at-

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[29] Pearson, "Walter Frank Raphael Weldon," 19.

[30] W. F. R. Weldon, "On Certain Correlated Variations in *Carcinus moenas*," *Proc. Roy. Soc.*, *54* (1893), 329.

tached considerable philosophical importance to Darwin's thesis, with its doctrine of slow progress achieved by never-ending struggle. This may be conjectured from his hostility to schemes of evolution by discontinuous variation, in which progress is the undeserved outcome of chance, and where struggle is the consequence of evolutionary advance (i.e., struggle between new, discontinuously formed varieties and existing forms) rather than its cause, and also from the sociological writings of his great friend Pearson, with whom he appears to have been deeply sympathetic. For example, in 1884, Pearson was to be found addressing an audience of working men, and telling them: "You may accept it as a primary law of history, that no great change ever occurs with a leap; no great social reconstruction which will ever benefit any class of the community is ever brought about by a revolution. It is the result of a gradual growth, a progressive change, which we term an evolution. This is as much a law of history as of nature."[31] This appears to indicate that Pearson was politically attached to Darwin's evolutionary gradualism. To accept the possibility of evolution by sports, one might suppose, was to admit what he did not wish to admit—that there was no natural sanction against successful revolutions.

This was the possibility which William Bateson, Weldon's former friend and pupil, openly advocated in 1894 in his *Materials for the Study of Variation treated with especial regard to discontinuity in the origin of species*.[32] In this work, Bateson, who was the most able of the advocates of evolutionary discontinuity, presented several strong objections to Darwin's views and presented evidence which, he hoped, would provide the basis for a new theory of evolution by discontinuous leaps. In his writings, Weldon seems always to have in view, as a goal, the refutation of Bateson's arguments.[33]

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31. Karl Pearson, *The Ethic of Freethought* (London, 1887), p. 320.

32. Bateson, *Materials for the Study of Variation.* A good account of Bateson's pre-Mendelian work is given in chapter one of E. A. Carlson, *The Gene: A Critical History* (London, 1966). See also W. Coleman, "Bateson and Chromosomes: Conservative Thought in Science," *Centaurus, 15* (1970), 228–314. Coleman is concerned primarily to explain Bateson's opposition to the chromosome theory, but in so doing gives an account of the development of Bateson's thought patterns.

33. Before his move to University College London in 1891 Weldon had been lecturer in invertebrate morphology at Bateson's Cambridge college, St. John's, and, according to Mrs. Bateson, was at the time Bateson's "most intimate friend." Weldon was instrumental in securing a grant for Bateson to study at the Chesapeake Bay Zoology Station under W. K. Brooks. Brooks,

Bateson had three main objections to Darwin's doctrine of evolutionary continuity[34] (i.e., the doctrine that new species did not suddenly appear, but were slowly built up by the natural selection of individual differences over many generations). Firstly, he argued that it was an observable fact that species could only be arranged in a discontinuous series and could not be arranged so as to form a continuous one. Species, he said, did not merge with their phylogenetic neighbors; there were marked interspecific differences. This was held to be inconsistent with Darwin's theory, which, presumably because of its emphasis on continuity, Bateson interpreted as asserting that "specific diversity of form is consequent upon diversity of environment, and diversity of environment is thus the ultimate measure of specific form." For, if this was the correct view, how could it be that while diverse environments often shaded into each other insensibly, forming a continuous series, the species which were subject to them usually formed a discontinuous series? Temperature, altitude, and depth of water, he observed, were "continuous in their gradations, while as a rule the forms of life are discontinuous."

In fairness to Darwin, it should be pointed out that in the *Origin* he had discussed an objection to his theory which was very similar to Bateson's: "why, if species have descended from other species by fine gradations, do we not everywhere see innumerable transitional forms? Why is not all nature in confusion, instead of the species being, as we see them, well defined?" [35] Bateson did not discuss Darwin's solution to this problem, but suggested that the discontinuity observable in nature might be "in the living thing itself"; that is to say, a reflection of the true nature of species-forming variation.

Secondly, Bateson argued that the characters which visibly

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unlike Weldon, was not committed to the evolutionary insignificance of discontinuous variation, and it appears to have been during his American period that Bateson formulated his notions of evolutionary discontinuity. (See W. Bateson and others, "William Keith Brooks. A Sketch of His Life by Some of His Former Pupils and Associates," *J. Exp. Zool.*, *9* [1910], 1–52.) Bateson's adoption of new ideas led to a rift with Weldon, for Mrs. Bateson records that "extreme divergence of their views undermined this friendship which later dissolved in bitterness." Weldon certainly studied all that Bateson wrote, as instanced by his unfavorable review of the *Materials* in *Nature*, 50 (1894), 25–26. It is interesting to note that Galton wrote favorably of Bateson's work in his "Discontinuity in Evolution," *Mind*, n.s., 3 (1894), 362–372.

[34] Bateson, *Materials for the Study of Variation*, pp. 1–17.

[35] Darwin, *The Origin of Species*, p. 321, sentences 6–7.

differentiated species were not as a rule "capital facts in the constitution of vital organs," but, more often than not, were "just those features which seem to us useless and trivial, such as the patterns of scales, the details of sculpture on chitin or shells, differences in number of hairs or spines, differences between the sexual prehensile organs and so forth." The force of this point was that it seemed impossible that these differences could have been produced, as Darwin suggested, gradually, by the "accumulation of innumerable slight variations, each good for the original possessor." For, in these cases, there seemed little reason for supposing that a species had a better chance of survival, under any environment, than did its phylogenetic parent.

Bateson's third objection to the theory of evolutionary continuity was based on the supposed imperfection of incipient structures. Although it seemed fairly obvious that many organs were useful to their bearers when in a perfected state, it was hard to see how these could have been of any advantage while in the incipient stages they had passed through if they really had been produced by the accumulation, by natural selection, of individual differences.

Darwin had, in fact, considered and replied to all of these objections to his thesis of evolutionary continuity. But Bateson did not discuss these replies, and suggested that the problems he had raised might be easily disposed of if one supposed that "the discontinuity of species results from the discontinuity of variation." In support of this hypothesis he presented, in the *Materials*, a collection of records of cases of what he termed "discontinuous variation." This act of collection distinguished Bateson from other sceptics. In practice, a "discontinuous variation" was a rare and noticeable deviation from the appropriate normal form—Bateson, in 1894, making no attempt to equate these variations with the sudden production of a new type of genetic element.

There is no need here to elaborate upon Bateson's classification of discontinuous variations into *meristic variations* (i.e., variations in the symmetry of creatures, or in the number of their repeated parts) and *substantive variations*, which were variations in the actual constitution or substance of the parts themselves. But it was certainly the case that some of the variations he found, such as the four-jointed tarsus of *Blatta americana*,[36] and the tulip having its flower parts in multiples

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[36] Bateson, *Materials for the Study of Variation*, p. 63.

of four rather than of three,[37] did suggest the sort of perfection which Darwin had been inclined to attribute to the effect of long-continued selection.

In the concluding section of the *Materials*, Bateson summed up his position. He did not suggest that any of his examples were more than "such as go to the building of specific differences," but argued that the existence of "sudden and discontinuous variation," the sudden appearance of variant forms exhibiting the kind of perfection of structure which Darwin had invoked evolutionary continuity to explain, "disposes once and for all of the attempt to interpret all perfection and definiteness as the work of selection." His view, one supposes, was, that as a rule new species were formed either all at once or by the accumulation of a number of discontinuous variations. If this were the case, then one could understand why species were sometimes differentiated by "trivial differences of feature." These would have arisen suddenly, and, if not harmful, would have maintained themselves in the population—given that Darwin's view of heredity as a blending process was not always a correct one.

This then was the background to Weldon's discussions of selective death rates. Exactly how many scientists supported Bateson's view of evolution as an essentially discontinuous process is perhaps beside the point. The point is that in his papers Weldon seems often to be addressing those who agree with Bateson, and, in particular, he seems anxious to refute the second and third of the arguments outlined. In his work we find Weldon attempting to show that the smallest and the most unlikely variations could make all the difference between survival and extinction in the struggle for existence, and that, accordingly, those who argued that specific differences could not have been formed by the slow accumulation by natural selection of small individual differences were quite simply wrong.

WELDON'S DEFENSE OF DARWINISM

Although the details of the events that led to its formation are difficult to discover, it is certain that in 1893 the council of the Royal Society appointed a Committee for Conducting Statistical Enquiries into the Measureable Characteristics of Plants and Animals, whose members were Galton (chairman),

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[37] Ibid., p. 61.

Weldon (secretary), R. Meldola, E. B. Poulton, A. Macalister, and Francis Darwin. Writing to Pearson shortly after Weldon's death (1906), Galton[38] said that the first he had heard of the committee was from Michael Foster, who told him that the council of the Royal Society had been asked to form one—Galton did not say by whom—and that they had decided to do so on condition that Galton acted as chairman, which he agreed to do. He wrote also that his main reason for accepting had been the hope that "the numerous bodies engaged in horticulture and zoology might in one aspect of their work, be coordinated by the committee and that research of a scientific kind might be introduced into the proceedings of each of them." In this hope he was to be disappointed. Even the committee itself was to suffer from a lack of proper coordination. Pearson relates[39] that, at the time of the committee's formation, Weldon had already begun to investigate the death rates of the crabs in Plymouth Sound.

The committee's first meeting took place on January 25, 1894, and, after some inconclusive work, published as its first report, in 1895, the "Attempt to Measure the Death Rate due to the Selective Destruction of *Carcinus moenas* with Respect to a Particular Dimension."[40] This contained Waldon's observations on the crabs in Plymouth Sound, and the conclusions he drew from them, and appended to it, was his short note "Remarks on Variation in Animals and Plants,"[41] which contained a defense of Darwin's thesis that evolution was a continuous rather than a discontinuous process.

SELECTIVE DEATH RATES

(i) First Attempts

In this first report, which was published in February 1895, Weldon undertook the difficult task of ascertaining whether selection took place between birth and the adult or reproductive phase in the crabs found at Plymouth. He proposed to do this by comparing "the frequency of abnormalities at various stages of growth with the frequencies of the same abnormalities in

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[38] Pearson, *The Life . . . of Francis Galton,* pp. iiia, 287.

[39] Pearson, "Walter Frank Raphael Weldon," p. 24.

[40] W. F. R. Weldon, "An Attempt to Measure the Death Rate Due to the Selective Destruction of *Carcinus moenas* with Respect to a Particular Dimension," *Proc. Roy. Soc.,* 57 (1895), 360–379.

[41] W. F. R. Weldon, "Remarks on Variation in Animals and Plants," *Proc. Roy Soc.,* 57 (1895), 379–382.

adult life, so as to determine whether any evidence of selective destruction during growth could be discovered or not." In other words, he was attempting to compare samples of a local race taken at early stages of growth with another sample taken from the adult population. This is obviously a difficult thing to do, because one has to allow for all the changes that are brought about in growth; and in order to draw any conclusions at all from his data, Weldon was obliged to make assumptions about the mode of growth of the crab which he was later unable to confirm. For all this, it was an imaginative paper that laid the foundation for future work, and is well worth discussing.

Using size as his only criterion of age, Weldon collected about 7000 female crabs varying in length from 7.0 to 13.95 mm (adult crabs, he wrote, were those "whose carapace length is from 40-50 mm or more") and in each case measured two dimensions; namely, the crab's "frontal breadth" and its "right dentary margin" (see Fig. 1).

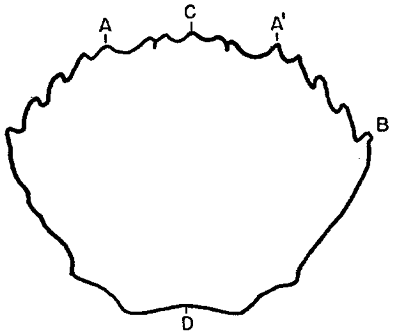

Fig. 1. AA' is the frontal breadth; A'B is the right dentary margin; CD is the total carapace length.

Each dimension was then measured in terms of a unit that was 4/1000 of the carapace length of the crab that bore it. It appeared that for an increase of 0.2 mm in carapace length, the mean associated frontal ratio always decreased by less than 4/1000, diminishing in growth from 853/1000 for crabs of carapace length of 7.1 mm to 604/1000 for crabs of adult size. Accordingly, Weldon arranged his crabs into 35 groups, with the individuals of each group differing by less than 0.2 mm in respect of their carapace length. The distribution of frontal ratios about the mean ratio did not give a very satisfactory approximation to the normal distribution in any of these groups, but Weldon was able to offer arguments to show that the discrepancies were due to the smallness of the samples. He concluded that "the law of frequency of variation throughout the whole series, may, as was hoped, be assumed to agree with the ordinary law of chance."

Table 1

—Quartile deviation of frontal breadths (Q) for various magnitudes of carapace-length (C)

C.	Mean Q. thousandths.
7•5	9•42
8•5	9•83
9•5	9•51
10•5	9•58
11•5	10•25
12•5	10•79
13•5	10•09
(Adult)	(9•96)

Source: *Proc. Roy Soc.* vol. 54.

From Weldon's point of view the most notable feature of the accompanying table was that it seemed to show that, up to an age represented by a carapace length of 12.5 mm, the quartile increased, but afterwards it diminished. He attributed the initial increase in variability to "the fact that average young produce on the whole average adults, while animals that exhibit a deviation of a known amount in the young state exhibit on the whole a greater deviation with advancing age," but admitted that this was a hypothesis that had still to be tested; and while acknowledging the possibility that the diminution in variability during late adolescence might be the normal mode of growth of the crab, decided to accept provisionally the hypothesis that "the diminution in the frequency of individuals of given deviation is due to selective destruction." He also assumed that in the cases of the Plymouth crabs and of other forms "which are sensibly in equilibrium with their present surroundings" the selection would act symmetrically about the mean, for which value it would be at a minimum.

This led to the possibility of a "demonstration" of the operation of a selective death rate during growth.

We were to suppose that at the period of maximum variability, the distribution of the deviations from the mean frontal ratio was representable by a normal frequency curve of modulus c_1 (see Fig. 2). Then, if k_1 was the height of the median ordinate, the whole number of individuals in the population would be $k_1\sqrt{\pi}\, c_1$. If the population was then subjected an an (unmeasurable in practice) unselective destruction, the modulus of the frequency distribution would be unchanged, but the height of the central ordinate of the frequency curve would be reduced to some other value k_2, and the total number of crabs to $k_2\sqrt{\pi}\, c_1$. The selective destruction[42] that took place during growth, Weldon argued, would have the effect of reducing the modulus of the frequency curve to some other value c_2, and would leave the central ordinate unchanged at k_2. In Fig. 2, the shaded area represents the "minimum number of individuals which it is necessary to destroy, in order to affect this reduction in the modulus," a number which is equal to $k_2\sqrt{\pi}\,(c_1-c_2)$. It followed that the ratio of animals selectively destroyed to animals surviving all unselective destruction was equal to $(c_1-c_2)/c_1$; which, for Plymouth crabs would take the value $(10.79-9.96)/10.79 = 0.077$, so that

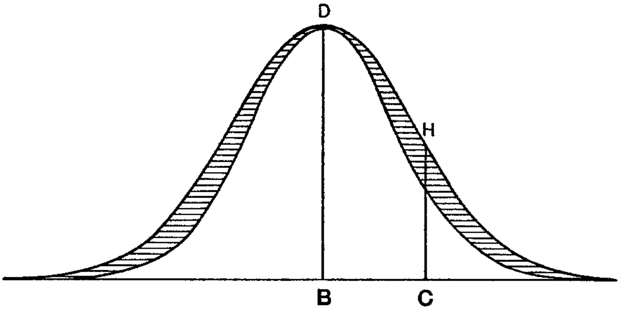

Fig. 2. DB = k. The inner curve has a modulus c_2; The outer curve has a modulus c_1.

> the hypothesis of selective destruction involves a death rate of about 77 per thousand between the ages corresponding to

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[42] In Weldon's terminology, if a population representable by a frequency curve with a median ordinate y_1 and a standard deviation (S.D.) σ_1 was reduced symmetrically about the median, to another with a median ordinate y_2 and standard deviation σ_2, then the death rate would be regarded as consisting of two parts—a nonselective part which reduced the population $y_1\ \sigma_1$ to the population $y_2\ \sigma_1$, and a selective part, responsible for reducing the population $y_2\ \sigma_1$ to the population $y_2\ \sigma_2$.

> 12.5 mm. in carapace length and maturity, as a consequence of deviation in frontal breadths, and in the group of structures, whatever they may be which are directly correlated with it.

Given Weldon's hypothesis, death rate was an easily determinable function of deviation. If we considered any ordinate (*HC*) of the preselection curve, letting its abscissa (*BC*) be of magnitude x, then the number of individuals falling in the interval, $x \pm \frac{1}{2}\delta x$, would be proportional to

$$e^{-x^2/c_1^2}\,\delta x,$$

but after selection it would have dropped to being proportional to

$$e^{-x^2/c_2^2}\,\delta x.$$

It followed, if one neglected the difference in constants, that the ratio between the number of individuals of deviation that were selectively destroyed and the number surviving unselective destruction was given by

$$\frac{e^{-x^2/c_1^2} - e^{-x^2/c_2^2}}{e^{-x^2/c_1^2}} = 1 - e^{x_2(c_2^2 - c_1^2)/c_1^2 c_2^2}$$

so that if g was the selective death rate among animals of deviation x, then the death rate varied according to the equation,

$$g = 1 - e^{-hx^2}, \quad \text{where } h = \frac{c_1^2 - c_2^2}{c_1^2 c_2^2}$$

and, said Weldon, in the case of Plymouth crabs, h was equal to "about 0.015."

Application of the same method to the data for the right dentary margin, Weldon argued, yielded no evidence of selective destruction. He found that, although the quartile did not increase uniformly with carapace length, the adult quartile was considerably greater than that of crabs of carapace length 12.5 mm.

Turning to Weldon's appraisal of his own results, we find that he was pleased to have obtained one of the results necessary for a determination of the direction and rate of evolution, without having to introduce any theory of the function of the organs concerned.

> Knowing that a given deviation from the mean character is associated with a greater or less percentage death rate in the animals possessing it, the importance of such a deviation can be estimated without the necessity of inquiring how that increase or decrease in the death rate is brought about, so that all ideas of "functional adaptation" become unnecessary.[43]

And, in the appendix to the report, he added that in just the same way as the importance of a given deviation could be estimated without inquiring how it affected the death rate, so, in a theory of heredity, a theory of mechanism was not necessary for one to be able to predict the value of the filial deviate which would be associated with a given paternal deviate.

In the same appendix, Weldon suggested that his results supported the view that specific modification was, at least generally, a gradual process resulting as Darwin had maintained from the accumulation of innumerable small variations, "each good for the original possessor." There was no need to think that change in specific character was an event that occurred only occasionally "as a capricious appearance of sports."

As might be expected, Weldon's paper was heavily attacked. Pearson tells that;

> The very notion that the Darwinian theory might after all be capable of statistical demonstration seemed to excite all sorts and conditions of men to hostility . . . The need for further investigation of the law of growth had been frankly admitted by Weldon in the remarks issued at the discussion of the report, but the critics declined to wait till further results were published.[44]

Much of this criticism, according to Pearson, was in the form of letters[45] sent directly to the committee, but there was also a considerable correspondence in the columns of *Nature*. Here Weldon's report was criticized by Ray Lankester,[46] by Karl Pearson,[47] and by J. A. Cobb.[48]

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[43] Weldon, "Remarks on Variation," p. 381.

[44] Pearson, "Walter Frank Raphael Weldon," p. 26.

[45] In the Galton papers, which are kept at University College London, there are several letters from Weldon to Galton which mention other, critical letters sent to the committee by Bateson. These letters are not very instructive, and so far I have not succeeded in tracing the letters which Weldon refers to. I would like to thank the Librarian for permission to examine these papers.

[46] *Nature*, *54* (1896), 245, 294, 366, 413.

[47] Ibid., 460.

[48] *Nature*, *55* (1896), 155.

Lankester's criticism was philosophical. He allowed that Weldon had shown the death rate among crabs to be selective, but upbraided him for not having tried to establish whether change in frontal breadth was the true cause of change in the death rate among crabs, or whether it was merely correlated with the variation of some other organ that was the true cause of change in death rate. Weldon replied, quoting Hume, and arguing that if one accepted that philosopher's account of causality, then, "the process of selecting one out of a group of universal antecedents, and calling that one alone the effective cause of the consequent, seems to me to involve precisely that knowledge that Hume and all his followers disclaim." However, in a later work on death rates, in which he tried to show that change in frontal ratio was a main cause (though not necessarily the only cause) of change in death rate, Weldon relaxed his position to the extent that he became prepared to discuss the relationship between only one of the "universal antecedents" and their consequent.

Pearson, for his part, denied that Weldon had demonstrated the operation of a selective death rate, pointing out that the report's conclusions rested on assumptions about the crabs' mode of growth that were both unproven and improbable. J. A. Cobb showed that, by applying Weldon's mathematical techniques to the statistics for the reciprocal of the ratio of frontal breadth of carapace length, one could obtain conclusions that were totally incompatible with Weldon's.

But what of the proposition to which Lankester had assented, namely, that Weldon had shown the death rate among crabs to be a selective one? We can see that Weldon had assumed in the report that, if there had been no selective death rate, then the young crabs which he examined would have grown into a population of adults with a mean ratio equal to that which he observed in the adults of Plymouth Sound, and with a quartile still equal to 10.97/1000. If these conditions were not met, then the mathematics of the paper would have been without foundation.

In the appendix to the report, Weldon admitted that he had assumed "a particular law of growth (which remains, as is admitted, to be experimentally tested)." Pearson relates that a lot of Weldon's time was spent in investigating the mode of growth of crabs, and that a report on this matter was submitted to the Evolution Committee in 1897,[49] but was never pub-

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[49] Pearson, "Walter Frank Raphael Weldon," p. 26. I would like to

lished. I have not succeeded in tracing this report, but judging from certain of Pearson's remarks,[50] it seems reasonable to suppose that Weldon found that the crabs' growth did not follow the simple pattern which he had assumed in the report. This perhaps is why, when delivering his presidential address to the zoological section of the British Association in 1898,[51] in which he gave account of further work on selection done with Herbert Thompson, Weldon requested his audience to disregard his previous report which "neglected several important facts which I now know."

In this address, Weldon again sought to demonstrate the operation of a selective death rate among crabs. However, instead of comparing statistics for young and adult crabs, and trying to prove selection with the assistance of hypotheses about the mode of growth of crabs, he instead adopted the policy of first showing that samples of crabs taken in Plymouth Sound between 1893 and 1898 showed certain changes in their vital dimensions, and then arguing that these changes were the *result of selection.* The very nature of his method obliged him to employ those considerations of "functional adaptation" which he had previously (reasonably plausibly) been able to regard as unnecessary.

In his address, Weldon argued that those who believed that "minute structural variations cannot in fact be supposed to affect the death rate so much that the theory of natural selection requires that they should," or that "many of the characters by which species are distinguished appear to us so small and useless that they cannot be supposed to affect the chances of survival at all" (surely a reference to Bateson and his followers!) were mistaken. And he undertook to convince his audience that, in the crabs taken from the beach below the Plymouth laboratory of the Marine Biological Association, ". . . small changes in the size of the frontal breadth do, under certain circumstances, affect the death rate, and that the mean frontal breadth among this race of crabs is in fact changing at a rate sufficiently rapid for all the requirements of the theory of evolution."

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thank the Librarian of the Royal Society for permission to consult the minute book and other papers of the Evolution Committee.

[50] Ibid. In a footnote, Pearson remarks that "no sufficiently general formula of growth can yet be applied to allow of the completion of Weldon's work in this direction."

[51] *Report of the British Association for the Advancement of Science* (1898), pp. 887–902.

As a first step, Weldon presented Table 2 reproduced below. It shows that the frontal breadth of Plymouth crabs was diminishing year by year. Obviously, all that the table by itself showed was that in Plymouth Sound, narrower crabs were becoming more common. Weldon's task was to show that this change was due to a selective death rate rather than to other causes, such as a correlation of fertility and narrowness, or the invasion of narrower crabs from somewhere outside of the Sound.

Table 2

The Mean Frontal Breadth Ratio of Male Carcinus mœnas from a particular patch of beach in Plymouth, in the years 1893, 1895, and 1898.

	Mean frontal breadth in terms of Carapace-length = 1000			
Length of Carapace	1893 (Thompson)	1895 (Thompson)	1898 (Weldon)	No. of crabs in the 1898 group
10·1	816·17	809·08	—	—
10·3	812·06	804·82	—	—
10·5	807·37	803·27	—	—
10·7	808·96	801·69	—	—
10·9	805·07	799·27	—	—
11·1	802·50	794·12	784·25	4
11·3	798·18	792·38	787·36	11
11·5	797·19	788·83	784·00	9
11·7	794·28	785·29	782·44	16
11·9	791·45	786·53	780·09	11
12·1	788·38	780·61	775·25	16
12·3	783·98	779·50	773·42	12
12·5	783·99	776·50	767·00	11
12·7	783·58	773·43	772·43	14
12·9	777·38	773·63	764·67	15
13·1	776·63	771·61	760·13	16
13·3	774·60	766·21	761·29	7
13·5	766·91	763·96	759·56	16
13·7	767·63	762·00	757·00	16
13·9	763·73	759·40	756·10	10
14·1	758·94	757·00	742·00	13
14·3	756·90	755·77	747·86	7
14·5	762·60	754·45	744·44	9
14·7	753·00	749·84	739·22	8
14·9	751·32	748·03	742·83	6

His strategy was to propose a hypothesis and to test it. He asked his audience to consider the recent history of the Sound and its environs, pointing out that for the last forty or fifty years a large breakwater had obscured its entrance, leading to an increase in the quantity of china-clay which, after being washed down from Dartmoor by local rivers, failed to get swept out to sea. The net result of this, combined with the increase in the amount of sewage which growing towns were emptying into the Sound, was that the water was becoming putrid and the seabed silted. This suggested that the fine silt in the water was selectively destroying broader crabs.

Weldon had experimented by keeping large numbers of crabs in vessels full of sea water in which was suspended "a considerable quantity" of china clay. He found that whenever the clay was as fine as that carried down from Dartmoor, "the crabs which died were on the whole distinctly broader than the crabs which lived through the experiment, so that a crab's chance of survival could be measured by its frontal breadth," and that when the clay was coarser, "the death rate was smaller and was not selective." The corollary of the hypothesis that the silt in the Sound was selectively destroying broader crabs was that if crabs were raised in silt-free water, they would be on the whole broader than the crabs raised in the Sound. Accordingly, Weldon established an apparatus of "some hundreds of numbered glass bottles, each bottle being provided with a constant supply of clean sea water by means of a system of glass syphons," and into each bottle he placed a crab taken from the beach. After each crab had moulted once, it was left to grow a new shell and was then killed: it was found, as hoped, that on the average the captive crabs were always broader than their feral fellows of the same length.

Weldon admitted that the policy of judging age by size, and of assuming that confinement did not pervert the growth of crabs, could well turn out to be a mistaken one; but he was pleased that all of his results were in accord with what might be expected if narrowness helped crabs to cope with fine silt. To further back the view that the observed population changes were the result of selection, he now introduced certain ideas of "functional adaptation" which in his previous paper (above, n. 43) he had hoped to avoid. He had found that, in his china-clay experiments, the gills of the dead but not of the survivors were covered with a fine white mud; and he thought it might be shown that, "a narrow frontal breadth renders one part of the process of filtration of water more efficient than it is in crabs of greater frontal breadth." One should not think of Weldon as contradicting himself. Previously, he had argued that under certain circumstances it was possible to know the extent to which a variation affected death rate without a theory about the way in which it did so. Now he was seeking to establish that certain changes in population dimensions were the outcome of selection. Clearly, to do this, he was obliged to produce all the evidence he could find which supported the view that these changes were due to selection and not to other factors.

In his peroration he maintained that he had presented a strong case for thinking that the diminishing relative frequency of broad crabs was the outcome of a selective death rate, due in turn to the greater filtering ability of the narrower crabs. This he took as support for Darwin's thesis of evolutionary continuity. The central difficulty of the theory of natural selection, he argued, was in believing that very small variations could be sufficiently harmful or useful to matter. This difficulty could only be settled by conducting experimental investigations of death rates.

Clearly, if we accept Weldon's tacit assumption that the laws of reproduction for Plymouth crabs were such that in the absence of selection at any stage in growth, the crab population would have remained stable in respect of its frontal ratios, then we must accept his claim to have demonstrated the operation of selection. We should be thankful for his attempt to explain the existence of this selective death rate. It is not the task of the scientist simply to show that two sets of phenomena are correlated (e.g., the sounding of a hooter in London and the emergence of factory workers in Manchester), he must also seek to explain the correlation—usually by showing it to be a logical consequence of some higher-level generalization for which there is more evidence than its own instances.

(ii) Pearson's Contribution

In 1900 Pearson published the second edition of his *Grammar of Science*. In the two new chapters on evolution, Pearson, among other matters, discussed the problem of determining empirically which value of an organ was the "fittest," or, to put it another way, which value had the best chance of survival.

As early on as 1896 Pearson had pointed out that the difficulties involved in discerning whether or not a population was undergoing selection during growth were very great. One would have to watch a generation from birth to the adult stage, "carefully preserving it from any form of selective mortality, such as arises from the struggle for existence," [52] and compare it—in respect of the organ(s) under discussion—with a similar

[52] Karl Pearson, *Phil. Trans. Roy. Soc., 197A* (1896), 257.

generation raised in its natural surroundings. The effect of selection, if any, would be revealed by the differences, if any, between the variation constants of the two groups at different stages in their growth. The problems were great, and in 1900 he recommended that, for the present, investigators should confine themselves to forms of life in which the adult stages were clearly marked, and deal only with selection that took place in that stage.

Obviously, in cases where the reproductive phase extended over a number of years, selection acting during the adult years could produce population changes as between one generation and the next, which it could not in cases, where, as in annual plants, individuals reproduced only once in a lifetime.

Pearson suggested that when trying to find whether the death rate was selective in respect of the various possible values of a particular organ, then, ideally, a group of "adult" animals would be measured and let go free for a time. At the end of the period, such of them as were still alive would be recaptured and recorded, and the differences between the means and the variances of the two sets of data calculated.[53]

In practice, however, he thought that the best that could be done would be to sample, say, 1000 adult members of a population, and to take another sample of 1000 at a later date and compare the two. We would, of course, "choose our type of life and its locality with reasonable precautions against migrations of any kind." After drawing the corresponding frequency polygons, one could then determine which value of the organ under consideration was the "fittest."

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[53] Karl Pearson, *The Grammar of Science* 2nd ed. (London, 1900), p. 408. In this work Pearson expounded his phenomenalistic philosophy of science. Weldon sympathized with Pearson's view that statements should be analyzed for their observational content. (Pearson, for instance, regarded scientific statements containing "theoretical" terms referring to unobservable entities—e.g., "atom"—as logically equivalent to a concatenation of statements which referred only to the sense impressions of some observer.) Thus we find Weldon consciously avoiding traditional Darwinian terminology, and instead of speaking of characters as being "useful" or "adaptive," he speaks only of their effect on death rate. This methodological outlook is surely another reason for Weldon's undertaking death rate studies; it must have impressed him with the necessity for analyzing Darwin's statements about "the great and complex battle for life" for their observational content, and also for testing this content empirically. Certainly the Biometricians were characterized by a devotion to mathematics and to the formulation of a metaphysics-free science. See, for example, the editorial to the first number of their own journal, *Biometrika* (1901). Pearson did not use the method he described in any field investigation of death rates.

The diagram of Fig. 3 gives, by the polygon $1,d,a,h,15$, the distribution of the organ under consideration at the time of the first sampling, and by the polygon $2,e,b,g,14$, its distribution at the second sampling. Pearson pointed out that that the total death rate reduces the original 1000 to $1/n$ of 1000, so that to get the actual distribution of the original 1000 adults after selection we should have to take $1/n^{th}$ of the vertical ordinates of $2,e,b,g,14$. Now, focusing upon individuals with a character value of 5, we see that the chance of such an individual's having survived is equal to $(e5/n)/d5$. If we now reduce the vertical ordinates of the polygon $2,e,b,g,14$ to $1/m^{th}$ of themselves, so that the new polygon, $2,f,c,i,14$, falls just inside the old one $1,d,a,h,15$.—i.e., they touch at only c—we have it that

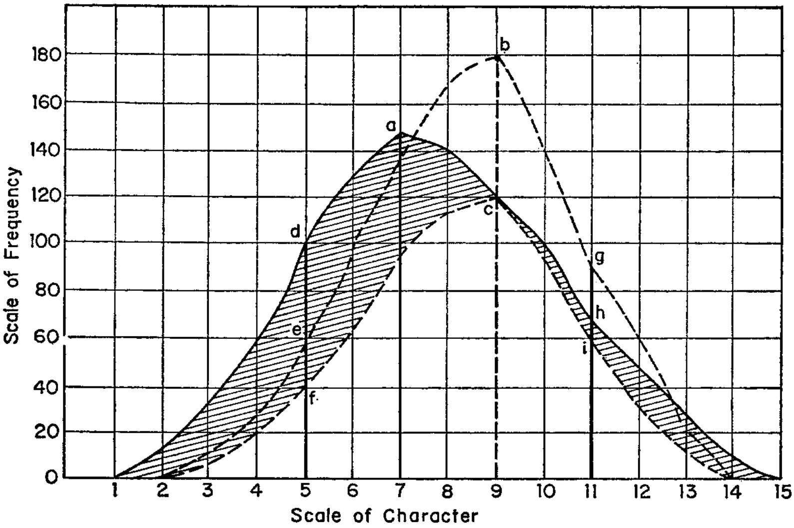

Fig. 3. Variation curves at different periods.

$$f5{=}e5/m, \text{ so that } e5/n = mf5/n;$$

also that $f5{=}d5{-}df$. Whence it follows that the chance of such an individual having survived is equal to

$$(m/n\cdot(d5{-}df))/d5 = m/n{-}(m/n)\cdot(df/ds))$$

And the corollary of this is that the chance of death for such an individual is equal to

$$1 - m/n + m/n \cdot df/d5$$ [54]

So, by inspection, it can be seen that the chance of survival is greatest at the point c where the two polygons touch. Thus, said Pearson, in his example, it would be the organ of size 9 that would be judged the "fittest."

In practice, the value of n would be unknown and all that could be determined would be the relative selective death rates for different sizes of organ. That for an organ of size 5 is to that for an organ of size 11 as $df/d5$ is to $hi/h11$.

Pearson acknowledged that groups of organs might be genetically linked. If this was the case, then a correlation between the size of an organ and death rate might in fact be due to the organ being genetically linked with another organ that was subject to direct selection. At the best, he wrote, "the determining of the actually selected organs will only amount to a highly probable guess." [55]

Two points of interest emerge from Pearson's work. Firstly, we see the way in which his phenomenalistic methodology led him to give an empirical definition to another Darwinian term the "Fittest." Second, his work exposes the tautological nature of the expression, the "Survival of the Fittest" for those that survive the best just *are* the fittest.

(iii) Weldon's snails

Pearson as we have seen, held back from discussing the problem of seeing whether selection operated between birth and the adult stage, Weldon, in his "A First Study of Natural Selection in *Clausilia laminata*" (1901)[56] found a case in which this could be done and again showed that, contrary to Bateson's views, the smallest and most unlikely variations could materially affect an individual's chances of surviving to reproduce.

Weldon's special case was the snail *Clausilia laminata,* whose shell is essentially a tube coiled about an axis, with successive coils in contact.

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[54] Pearson spoke of the death rate as composed of two components: a constant part, $(1-m/n)$, and a selective part, $(m/n.\mathrm{df}/\mathrm{d5})$.

[55] Pearson, *The Grammar of Science,* p. 408.

[56] W. F. R. Weldon, "A First Study of Natural Selection in *Clausilia laminata,*" *Biometrika, 1* (1901), 109–124.

The convenience of *Clausilia* lies in its shell. The upper whorls of an adult's shell represent the condition of the young shell, from which the adult shell was formed by the growth of additional whorls. This made it possible to compare the shells of young snails with the upper whorls of the shells of adult snails, in order to see whether, in respect of a particular shell character, the snails surviving to adulthood were a random or nonrandom selection of young snails.

In his paper, Weldon discussed a large sample of shells which he had taken from a lakeside in eastern Holstein. Both young and adult shells appear to have been gathered at the same time.

The character he considered as a complex one. First of all, he defined the columellar and peripheral spirals of the shell. "Peripheral spiral" was the name given to the line of contact of successive whorls along the outside of the shell; "columellar spiral" was the name given to the line of contact along the axial wall. This done, he defined as a reference plane, the plane passing through the axis of the shell that contained a radius of the columellar spiral exactly 5 mm in length, i.e., *AC* in Fig. 4. By great ingenuity, and by sectioning 200 shells,

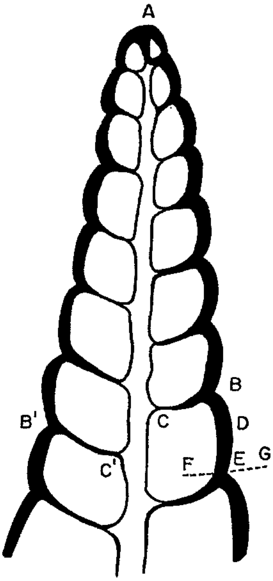

Fig. 4. Section of *Clausilia laminata*. Suppose AC = 5 mm.

he was able to draw up tables, giving for young and adult snails the mean lengths of the peripheral spiral located by rotating the peripheral radius vector through fixed numbers of right angles from the reference plane.[57]

In Table 3, angular distances from the reference plane, i.e., the "Standard Columellar Radius," toward the shell-apex are entered as negative, and those toward the shell-mouth as positive.

Table 3

Mean Peripheral Radius at Corresponding Points on the Spiral of 100 Young and 100 Adult *Clausilia.*

Angular distance from standard Columellar radius in right angles	Mean peripheral radius	
	Adult	Young
— 19	0·8820 mm.	0·9022 mm.
— 17	1·1251	1·1350
— 15	1·3889	1·4044
— 13	1·6820	1·6903
— 11	1·9996	2·0229
— 9	2·3463	2·3630
— 7	2·7336	2·7521
— 5	3·1529	3·1666
— 3	3·6265	3·6297
— 1	4·1397	4·1254
+ 0·9810	4·7181	4·6952

Source: *Biometrika,* vol. I.

The differences in means were in no case significant, and Weldon concluded that there was "no evidence of change in the mean character of the peripheral spiral during growth." This left only the variances of the young and adult spirals to be compared.

To this end he was able to calculate the standard deviations of the arrays of peripheral radii corresponding to fixed values

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[57] The distance of the plane of section from the reference plane was determined as follows: Suppose that in Fig. 4 *AC* was not 5 mm but 4.68 mm long, and that the next columellar radius *AC'* was 5.27 mm long. Then, assuming that the columellar spiral was sensibly equiangular through 180°, the angle between the section and the reference plane would be

$$\frac{5 \quad - 4.68}{5.27 - 4.68} \times 180^\circ = 0.5424 \times 180^\circ.$$

Since all measures in any section were 180° apart, the position of one relative to the reference plane determined that of all the others.

of the angular distance from the reference plane. He found that, during the six right angles of revolution immediately above the reference plane, the excess variability of the young shells over the old was highly significant (Table 4).

His conclusion was that there was a selective death rate during growth, but one which selectively eliminated the more extreme variants on either side of the mean peripheral radius. Here was a case where natural selection was not so much changing the character of a local race as keeping it crisply defined.

Table 4

Values of r_{xy}, σ_y and $\sigma_y \sqrt{1 - r^2_{xy}}$ for corresponding groups of peripheral radii in young and in adult-shells from Gremsmühlen.

Angular distance from Columellar radius in right angles	r_{xy}		σ_y		$\sigma_y \sqrt{1 - r^2_{xy}}$	
	Adult	Young	Adult	Young	Adult	Young
— 8 to — 10	0·7527 ±0·0292	0·7922 ±0·0251	0·120849	0·140872	0·07956 ±0·00379	0·08597 ±0·00412
— 6 to — 8	0·8068 ±0·0235	0·8347 ±0·0202	0·133731	0·153473	0·07901 ±0·00377	0·08388 ±0·00402
— 4 to — 6	0·8534 ±0·0183	0·8622 ±0·0173	0·134119	0·154627	0·06991 ±0·00333	0·07833 ±0·00375
— 2 to — 4	0·8726 ±0·0161	0·8782 ±0·0154	0·146252	0·168564	0·07143 ±0·00341	0·08062 ±0·00386
0 to — 2	0·9290 ±0·0092	0·8800 ±0·0159	0·156270	0·170469	0·05784 ±0·00276	0·08096 ±0·00388
0 to 2	0·9415 ±0·0077	0·9367 ±0·0105	0·170046	0·173881	0·05732 ±0·00273	0·06087 ±0·00292

Source: *Biometrika*, vol. I.

He also proposed that selection was "periodic," that is, he thought that while the parents of a generation were always a selection of adolescents, the variability of parents and adolescents would remain constant from one generation to the next.

Weldon hypothesized that the selection was "indirect,"—". . . that is to say the life or death of an individual is determined in each case by the value of a (probably large) number of correlated characters, of which length of the peripheral radius is only one."

Further support for his view that the life or death of an individual could depend on structural differences as slight as that described, was provided by some observations of the ecology of a beech wood near Monk's Risborough in Buckingshire. Here he found that while the closely related *C. nigricans* could live in the wood *and* in the surrounding hedgerows and meadows, it appeared that *C. laminata* could live only in the wood; and yet the differences between these two species were ". . . (1) a difference in size; (2) a difference in the pitch of the spiral; and (3) other slight differences in the shape of the shell and of various organs." [58] Although these differences seemed to be of little importance, they were demonstrably associated with an "enormous difference in susceptibility to certain environmental differences." Because this was the case, argued Weldon, he was justified in accepting evidence that pointed to a correlation between variation in death rate and the variation of a character within the limit of one species, even though he was, for the present, quite unable to imagine the process by which this correlation was brought about. He had, however, demonstrated the essential Darwinian point that which snails lived and which died was not determined by chance alone.

This result robbed one of Bateson's arguments of much of its force. Bateson had contended that new species must often have arisen suddenly, because the differences between a species and its phylogentic parent often appeared so unrelated to utility that it seemed impossible to conceive that they had been produced by the gradual accumulation by natural selection of innumerable slight variations. Weldon's work showed that the most insignificant-seeming variation might be associated with differing chances of surviving to reproduce, a result which,

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[58] Weldon, "A First Study," p. 124. I would like to thank Dr. R. C. Olby of the University of Leeds for having drawn my attention to the work of H. C. Bumpus, who also studied death rates. See, e.g., his "The Elimination of the Unfit as Illustrated by the Introduced Sparrow *Passer domesticus*," *Woods Hole Mar. Biol. Lab. Lect.* (1898), 209–226. Bumpus's work is discussed in chap. 7 of J. Maynard Smith's *The Theory of Evolution* (Penguin Books, 1958). His result was similar to Weldon's in that he found evidence of a selective elimination of extremes. With selection following this pattern, one might expect the successive generations of a population to become less and less variable, but Smith explains why this process does not lead necessarily to genetic uniformity among a population's members. Weldon, in his paper, did not mention the work of Bumpus. It is interesting to note that in his later paper, "Note on a Race of *Clausilia itala*," *Biometrika*, 3 (1903), 299–307, Weldon reported that he had been unable to find evidence of selective destruction among the *C. itala* taken from Brescia.

when taken in conjunction with Pearson's refutation[59] of Galton's theory of perpetual regression,[60] went a long way towards demonstrating the possibility of the truth of Darwin's views.

Unfortunately, the Biometricians had no convincing reply to Fleeming Jenkin's earlier criticism of the Darwinian thesis,[61] that there appeared to be rigid upper limits set by nature to the degree of change which could be produced by selective breeding from individuals showing extreme values of individual differences. As I hope to show at a future time, this problem would remain unsolved until it was recognized that biometric laws of ancestral heredity could be explained in Mendelian terms.

Based on an M.Phil. thesis, *Theories of Evolution of the Biometric School,* which I wrote in the Department of History and Philosophy of Science, Chelsea College, University of London. My researches were carried out on a Science Research Council grant. I would like to thank Dr. M. P. Earles of Chelsea and Professor J. S. Wilkie of University College London for many helpful suggestions—but I would point out that any errors are my responsibility alone. I would also like to thank the editor and referees for helpful comments on an earlier draft of this paper.

[59] See above, nn. 24–27.

[60] See above n. 18.

[61] See above, n. 9. Galton in 1879 (see above n. 18) had offered what was in effect a mathematical reformulation of Jenkin's point, but it was formulated in ignorance of the mathematics of multiple regression. These are explained in C. E. Weatherburn, *A First Course in Mathematical Statistics* (Cambridge, 1968), pp. 242–260.