The Distribution of Variation Before, During and After Speciation

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ABSTRACT

Francis Galton and Charles Darwin both came to consider Quetelet's law of error, now the normal curve, to be the best model for the distribution of variation in the characters of species where there is little pressure to survive. The initial focus for Galton was the distribution of abilities in humans and in this context he speculated that pressures arising from artificial selection, specifically differential birth rates across the social strata, distorted the distribution. He did not concern himself directly with the distribution of variation as species separate, though it is possible to picture the shape of the distribution implicit in his discussion of saltationism. Charles Darwin argued in *Nature* that, under changed conditions, the symmetry of the distribution would be lost around the point at which species separate but his son, George Darwin, showed how the symmetry would be restored. By a different argument, George Romanes also explained that the symmetry of the normal distribution would return and, with his analysis, Galton was in full agreement.

Galton on the distribution of abilities before, during and after eugenic intervention

In *Hereditary Genius*, published in 1869, Galton extended Quetelet's use of the error law to model the distribution of abilities in humans. His interest was in the extent and manner in which intelligence was ranged in the population and how it might be transmitted from one generation to the next. Whilst he had nothing to say about animal species, he did draw conclusions about different races in man. And whilst he had nothing to say about natural selection, he viewed class-driven artificial selection as a threat to society. Specifically, Galton modelled the distribution of abilities of different races using normal curves of different means but the same degree of dispersion and he identified particular racial groups as falling one or two grades below that of the English. The idea of 'overlapping' distributions he also adopted to visualise and explain the distribution of a single people's abilities over time. Galton envisioned this as a shift in the mean, but with no adjustment to the dispersion, arguing that 'If we could raise the average standard of our race only one grade, what vast changes would be produced!'[1] At this time, Galton paid relatively little attention to the magnitude of the dispersion, partly because there was no way of measuring it and partly because he was yet to make the shift from the essentialism of Quetelet to the population thinking of Charles Darwin.

In January 1873, Galton discussed the loss and return of the normal curve in 'Hereditary improvement', a rather pessimistic postscript to *Hereditary Genius*.[2] Here, he argued that the great, civilized nations did not have a sufficient number of eminent men to carry out the responsibilities of leadership. The deterioration, in mental and physical attributes alike, resulted from numerous 'mischievous influences of artificial selection', including differential birth rates.[3] The 'average worth of our race [is] debased … from its typical level by those deleterious influences of modern civilisation'.

As Galton saw it,

> the pick of our present race would not be symmetrically arranged, but the worst of them would be the most numerous and the form of the whole body, when classified, would be that of a cone resting on its base, whose sides curved upwards to a sharp point.[4]

It appears that he envisaged the distribution to be deficient in the upper ability range, skewed towards the lower talents, having both a reduced average and a reduced dispersion. Following Pearson's terminology of 1906, we would term it positively skewed and leptokurtic.

Galton went on to argue that this distorted distribution will only return to its familiar symmetrical shape when a eugenic programme is instituted:

> [T]he distribution of ability in a race so improved, would be very different to that of the pick of the present race, though their *average* worth was the same. The improved race would have its broad equatorial belt of mediocrities, and its deviations upwards and downwards, narrowing to delicate cusps; but the vanishing-point of its baseness would not reach so low as at present, and that of its nobleness would reach higher.[5]

This is a perfect description of a normal curve, symmetrical and mesokurtic. By 1873, Galton saw pressures on a population, arising from artificial selection, as having the effect of skewing the distribution of abilities, and the removal of those pressures as essential for restoring the normal distribution.

Galton's rough stone

In his attempt to understand the manner and extent of intellectual inheritance, Galton developed a theory of transmission of characters from generation to generation in man. It was a theory stated in terms of molecules and their interactions, according to Herbert Spencer's *Principles of Biology*.[6] Though there are traces of the theory in a paper of 1865, Galton's ideas developed further in response to Darwin's Theory of Pangenesis, published in 1868, and reached final form in the period 1872-1876.[7] There is a critical difference here between the theories of Darwin and Galton. Darwin used the term 'pangenesis' to indicate that the body tissue in general was capable of 'throwing off' gemmules, whilst Galton's 'germs' were created only in the reproductive organs. We cannot explore Galton's theory in any greater detail here. Its immediate importance for Galton's statistics is that the germs behave as particles in physics. Their organisation, Galton argued, 'wholly depends on the mutual affinities and repulsions' to which they are subjected 'during all the processes of their development'.[8] By constructing a theory that was based on a fundamental unit of transmission, he was appealing directly to traditions in probability and mathematical physics. I have previously argued that Galton's atomism is central to understanding the development of his statistical innovations.[9] The specific emphasis here is on the role of the theory for the stability of types and what this tells us about Galton's picture of the changing distribution of variation around the point at which species separate.

If there was indeed a difference between Galton and Darwin on the mode of transmission of characters, there was a more fundamental difference in respect of the way in which species separate. In the *Origin of Species* published in 1859, Darwin considered evolution as taking place in a multitude of tiny random steps that prove favourable to a species under certain pressures, and now referred to as continuous variation. Galton favoured discontinuous variation or saltationism in which the steps are fewer and larger, and he was far from alone in this; some of Darwin's inner circle including Huxley took this position.[10]

In a section on 'Stability' at the end of *Hereditary Genius*, Galton invoked the notion of a 'rough stone' to explain why an uncountable number of 'insensible gradations' were wholly unnecessary when 'one type yields to another'. This rough stone would have:

> in consequence of its roughness, a vast number of natural facets, on any one of which it might rest in "stable" equilibrium. That is to say, when pushed it would somewhat yield, … [but] on the pressure being withdrawn it would fall back into its first position. But, if by a powerful effort the stone is compelled to overpass the limits of the facet on which it has hitherto found rest, it will tumble over into a new position of stability, whence just the same proceedings must be gone through as before, before it can be dislodged and rolled another step onwards. The various positions of stable equilibrium may be looked upon as so many typical attitudes of the stone, the type being more durable as the limits of its stability are wider.[11]

So, he would come to link the error law of traits and characters with the equilibrium associated with the major facets, the width of the facet (the amount of variation) determining the degree of stability. Galton would return to this allusion of the polyhedral stone again and again. The only diagram of Galton's polyhedral model is to be found in his 1889 synthesis, *Natural Inheritance*; it makes its appearance in the third chapter, which is devoted to 'Organic Stability'.[12]

FIG. I.

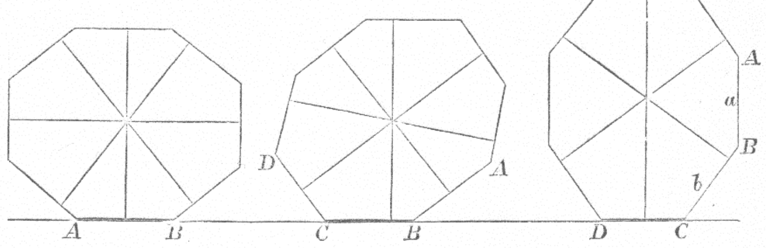


Figure 5.1: Galton's polygonal slab, as drawn in *Natural Inheritance*

On the left we see the slab in its 'primary' position of stability, resting on AB. Simple deviations from the type will tilt the slab to the left or right but will prove insufficient to shift the slab onto an adjacent face. But if the force is sufficiently powerful the slab will come to rest on BC say, a 'subordinate' position of stability. From this face, it falls back with comparative ease to rest again on AB or is pushed by a massive force onto CD. Pushed further, the slab topples helplessly through what would be DE had Galton continued his labelling of the figure, towards a position, not shown, in which the slab is upside down, resting on what would be EF. Position AB is indicative of the type, tilting and reverting to AB illustrates 'variability within narrow limits without prejudice to the breed', BC and CD are examples of 'partly stable sub-types', EF is an 'occasional sport which may give rise to new types'.[13] There is no room in this theory for intermediate forms.

There is enough here to conclude that Galton considered that under normal conditions of life the distribution of variation is normal, that the symmetry is lost under pressure (asymmetric (skewed), reduced dispersion and with a more prominent peak (leptokurtic)) and these features increase to the point of speciation and suddenly adjust thereafter to patterns similar to before but with a displaced mean.

The plenitude of variation exhibited by the barnacles

Variation played a central role in Charles Darwin's theory of evolution and its abundance was a key to his final understanding of evolutionary biology. In the autumn of 1846, Darwin dissected a minute sessile barnacle that he had discovered sunk into the shell of a mollusc, in the Chonos Archipelago off Chile's western seaboard.[14] Possessing a complex life cycle and the most unconventional sexual dimorphism, the barnacle threw up such difficult questions of classification that Darwin decided to extend the study to related species. Thus began eight years of painstaking examination and classification that culminated in the publication of a definitive four-volume reference work on the taxonomy of living and extinct cirripedes.[15] It was Darwin's research on barnacles that revealed the plenitude of variation and this led inevitably to the complex question of where variation within species ends and the separation of species begins. It was a question made no easier by the fact that 'the cirripedia are very troublesome from their great variation'.[16]

Darwin's understanding of variation emerged over a lengthy period of time; by 1854, he realised that divergence is accentuated wherever the competition for resources is keenest, for only in these conditions is the pressure to specialize at its greatest. In the fifth chapter of *Origin of Species*, which is devoted to 'Laws of Variation', Darwin argued that variation results directly from the effects of changed conditions on the reproductive process. The struggle for existence is greatest among members of the same or closely-related species, since differing little they depend on the same resources. In a substantial section on the effects of use and disuse Darwin stated that

> If under changed conditions of life a structure before useful becomes less useful, any diminution, however slight, in its development, will be seized upon by natural selection, for it will profit the individual not to have its nutriment wasted in building up an useless structure.[17]

In 1860, the year after the publication of *Origin of Species*, Darwin began work on *Variation of Animals and Plants under Domestication*. This was intended to be the first part of a two-part project on variation — the sequel on variation in nature was never written — with the object of providing evidence of the plenitude of variation available to natural selection.[18] Statistical arguments, as such, still played no part whatsoever. At this point, it was the degree of variation, rather than its distribution, which was discussed.

Charles Darwin's adoption of the 'law of error'

Despite making use of the statistical concepts of populations, variation, frequency distributions and correlation, the statistical approach to enquiry was not Darwin's preferred route to understanding nature.[19] Statistics influenced his evolutionary ideas far less than his evolutionary ideas subsequently influenced statistics.

Darwin was somewhat familiar with the 'law of error' (later the normal distribution) prior to his letter to *Nature*, though the extent of that familiarity is unclear. He was certainly aware of the arguments in Quetelet's *Sur l'Homme*, for an entry in his Notebook D in September 1838 records the fact that he read the 1835 review in the *Athenæum*.[20] Silvan Schweber argued that Darwin turned 'to Quetelet's work, probably to look for a quantitative statement relating to variations' and he followed up the review by acquiring a copy of the book.[21] However, *Sur l'Homme* treated statistical regularities and Quetelet's first anthropometrical application of the normal distribution appeared in *Lettres* in 1846. Darwin may have read Herschel's essay review of the book which was published in the *Edinburgh Review* in 1850.[22] It is also possible that he learnt more about the curve from his friend William Spottiswoode (1825-1883) who attempted somewhat unconvincingly to fit a normal curve to the heights of mountains in 1861.[23] Any shift in Darwin's familiarity with the law of errors from a simple awareness to a basic understanding resulted from his contact with Francis Galton (1822-1911) and his writings, and through the support of his son George Darwin (1845-1912). When *Hereditary Genius* was published in 1869, the opinion Galton most eagerly awaited as author was that of his cousin.[24] Charles Darwin's praise for the early part of the book was effusive. He wrote in December 1869 that

> I have only read about 50 pages of your book…but I must exhale myself, else something will go wrong in my inside … George, who has finished the book, and who expressed himself in just the same terms, tells me that the earlier chapters are nothing in interest to the later ones! … You have made a convert of an opponent in one sense, for I have always maintained that, excepting fools, men did not differ much in intellect, only in zeal and hard work; and I still think [this] is an eminently important difference. I congratulate you on producing what I am convinced will prove a memorable work.[25]

It was that early part of the book that Charles Darwin had already devoured that Galton explained his adoption of the normal curve as a model for the distribution of abilities. Whilst there is nothing to suggest that Darwin ever grasped the mathematical technicalities of the exponential function, by the early 1870s he had recognised the consequences of the law for evolutionary biology. And certainly, the linking of species separation and the loss of symmetry in a frequency distribution, in his letter to *Nature*, is of singular importance.

Symmetry lost: Charles Darwin's letter to *Nature*

Charles Darwin claimed that, under favourable conditions of life, the variation in an animal's organs and parts is distributed according to Quetelet's frequency law. In a letter to *Nature* in 1873 Darwin asserted that, where conditions are unfavourable, there occur evolutionary changes leading to the separation of species, together with a departure from Quetelet's law for some characters.[26] Following an exchange of letters, his son George contributed a supplementary, elucidatory letter to the same journal a few days later. He explained that, according to his father's theory, differential mortality rates could both displace the central value of the distribution of variation and spoil its symmetry, though ultimately that symmetry would be restored.[27] The cessation of a selective influence would have much the same effect on the distribution of variation, according to George John Romanes (1848-1894) in subsequent letters to *Nature*.[28] Eileen Magnello has drawn attention to the significance of Charles Darwin's letter for Weldon's work on dimorphism and ideas of speciation on the development of Karl Pearson's statistical thinking.[29] The role of George Darwin in support of his father's understanding of the distribution of variation was revealed in my doctoral thesis.[30]

Darwin's writing to *Nature* was prompted by an account by Charles Wyville Thomson (1830-1882) of the complemental males of the cirripede, *Scalpellum regium*, which had appeared in the journal on 28 August 1873.[31] The description of the anatomy of these large barnacles, hauled from the depths of the Sargasso Sea by the trawl nets of the *Challenger*, offered independent and reliable evidence of the extremes of variation which the cirripedes exhibited. In the final paragraph of his letter, Darwin wrote that it is

> known from the researches of Quetelet on the height of man, that the number of individuals who exceed the average height by a given quantity is the same as the number of those who are shorter than the average by the same quantity; so that men may be grouped symmetrically about their average with reference to their height … So it is with the circumference of their chests; and we may presume that this is the usual law of variation of all the parts of all the species under ordinary conditions of life. That almost every part of the body is capable of independent variation we have good reason to believe, for it is this which gives rise to the individual differences characteristic of all species.[32]

Specific appeal was made only to the rather more limited symmetry requirement but the allusion to Quetelet, to the particular applications made in *Lettres* (heights and chest girths) attests to his full adoption of Quetelet's law as the distribution of variation. However, if 'ordinary conditions of life' throw up normal distributions then, argued Darwin, natural selection upsets the symmetry, for

> it does not seem improbable that with a species under unfavourable conditions, when during many generations, or in certain areas, it is pressed for food and exists in scanty numbers, that all or most of its parts should tend to vary in a greater number of individuals towards diminution than towards increment of size.[33]

That is, the mean is reduced and the symmetrical normal distribution replaced by a distribution skewed to the left.

Symmetry regained: George Darwin's elucidation

In the days immediately after the publication of Charles Darwin's letter to *Nature*, George wrote to his father with a critique of its argument.[34] Though he made no comment on the subject, George may have initiated the move himself in a protective filial gesture, providing in advance the counter-arguments that would be needed if the letter provoked unfavourable reaction. Alternatively, if it were penned in response to his father's specific request, it was certainly not the first such appeal for specialist help that George had received.

The further development of the theory of natural selection and the enunciation of theories of heredity required a greater focus on mathematics and statistics. The leading investigators, Charles Darwin, Alfred Russel Wallace (1823-1913) and Francis Galton, lacked the expertise to undertake mathematical work of any complexity. This niche was filled by George Darwin.

George was most fortunate to have been taught mathematics at school by a gifted mathematician, Charles Pritchard (1808-1893). He had obtained a scholarship to Trinity College, Cambridge where neither his talents nor diligence manifested themselves initially. But under the tutelage of the distinguished coach, Edward John Routh (1831-1907), he had graduated in 1868 as Second Wrangler in the Mathematics Tripos and added the Second Smith's Prize.[35]

At Down, the Darwin family home in Kent, Charles encouraged his children to take an interest in his own researches and the activities of his scientific circle. In the period following George's graduation from Cambridge, Charles Darwin turned to him three times to help counter criticism of arguments put either in the *Origin of Species* or in *Variation of Animals and Plants under Domestication.* The subjects of these arguments were (i) the sterility of hybrids (ii) the availability of time for evolution to have taken place (iii) the likely number of elephants descended from a pair 500 years ago. George's consideration of the first bears directly on subsequent letters to *Nature* in 1873.[36] Just down from Cambridge he may have been, but George was touted by his father as someone who could apply mathematical reasoning to almost any subject, including the theory of evolution.

The question on the differential sterility of hybrids was raised by Wallace who expressed concern about Charles Darwin's 'objection to sterility between allied species having been aided by Natural Selection'.[37] He subsequently asked him to consider a number of cases, including

> the more difficult case of two allied species A, B in the same area, half the individuals of each (A^S B^S) being absolutely sterile, the other half (A^F B^F) being partially fertile: will A^S, B^S ultimately exterminate A^F, B^F? … To avoid complication, it must be granted that between A^S and B^S no cross-unions take place, while between A^F and B^F cross-unions are as frequent as direct unions, though much less fertile.[38]

Troubled by the complexities of Wallace's question but also pressed for time, Charles Darwin replied that, 'I have tried once or twice & it has made my stomach feel as if it had been placed in a vice'.[39] Three of his children had grappled with the question, he wrote, and 'my second son, the mathematician, thinks that you have omitted the almost inevitable deduction which apparently would modify the result. He has written out what he thinks, but I have not tried fully to understand him.'[40] George's partly mathematical argument took the following line. If inside a particular area there are sterile individuals of some species and outside relatively fertile individuals, then in the next generation, whilst the proportions of pure forms remain unaltered inside and out, because there are fewer hybrids inside than outside, the overall numbers inside the area are depressed. One consequence is that any pressure on limited resources will result in immigration into the area. Wallace disagreed, arguing that since the pure forms inside the area constitutes a higher proportion of the overall numbers than they do outside and since pure forms are better adapted to their environment, numbers inside the area will rise and any migration will take place in the opposite direction.[41]

When Charles Darwin's letter appeared in *Nature*, George was well placed to make a judgement on his father's hypothesis of a departure from Quetelet's law. His conclusion was uneqivocal: 'I fail to see how the law of distribution about a mean affects this argument.'[42] As an example, he took the lengths of the horns of a breed of cattle and allowed their distribution to be symmetrical among the well-nourished members of the breed. By contrast, he argued, the horns of a greater proportion of the ill-nourished members of the breed would be shorter and

> this w[oul]d have the effect of slightly reducing the average length of horn in ill fed cattle while at the same time the distribution about this average so reduced w[oul]d no longer be symmetrical, the shading on the lower side w[oul]d die away more slowly than on the upper side. [43]

There are two cases to be considered. Firstly, 'if the horns are useful those with shortened horns will be weeded out by Nat[ural] Sel[ection] & the tendency to diminution of horns in the whole race will thus be checked'. Furthermore, 'the weeding effects … will have a tendency to restore the symmetry of distribution about the slightly reduced average'. Secondly, 'if the horns are useless those with shortened horns will not be weeded out & the average length of horns will be yet further shortened in the whole race below the point to wh[ich] the direct effect of ill conditions had at first brought it.' In this case

> there will also be a tendency to restore the symmetry of distribution but it will take place thro[ugh] the short-hornedness being distributed by inheritance thr[ough]out the whole race & thus augmenting the diminution of length of horn thro[ugh]out & thus still further displacing the average

length of horn (i.e. the dark shade in the diagram) which was at first only slightly displaced thro[ugh] the direct effect of poor conditions.[44]

To make the argument clearer to his father, the letter ended with scribbled graphs, contrasting the initial distributions of horn length under favourable and unfavourable conditions and illustrating the symmetrical distributions towards which restoration takes place. The heaviness of the sweeps of the pen indicated the relative frequency. For further clarity a modern-day interpretation is also given. Here we imagine the sketch rotated through a quarter-turn clockwise and append impressions of the distributions.

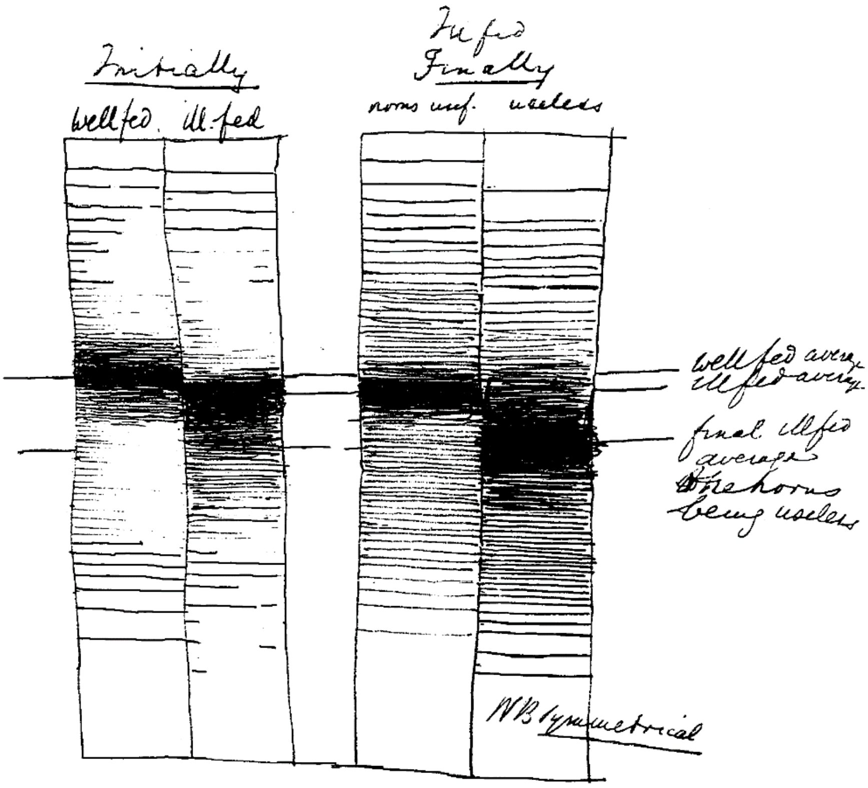
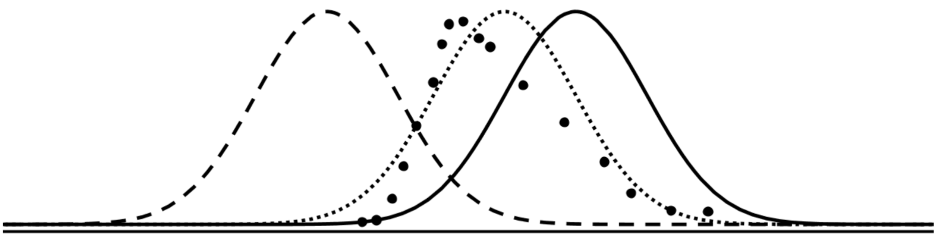


Figure 5.2: George Darwin's sketch distributions



initially well-fed	Normal distribution
initially ill-fed	Positively-skewed distribution with reduced mean
horns useful	Normal distribution with same reduced mean
horns useless	Normal distribution with twice-reduced mean

Figure 5.3: Modern-day interpretation of George Darwin's sketch distributions

If Charles Darwin was suggesting that species separation might be marked by a departure from Quetelet's law, then George Darwin believed that such a departure would be comparatively short-lived, for natural selection has a tendency both to destroy the normal distribution of variation and to restore it. Writing again to his father within a matter of days, George reassured him that the letter published in

Nature ‘expresses your meaning clearly’.[45] However, further elucidation would be ‘worth while, since everything you write attracts so much attention, that it is a pity to let people break their heads over their meaning’. His own critique, now redrafted in the form of a letter would serve such a purpose and it was enclosed for emendation. Charles balked at claiming ownership of the extended argument and suggested how the second letter might be suitably worded.[46]

George’s letter to *Nature* was dated 5 October 1873 and was published in the 16 October issue. There were only minor textual differences from the critique he had offered his father. The letter began by discussing the distribution of the heights of ‘several thousand men of the same race’, their relative frequencies being described in terms of pins in a wall. This was Quetelet’s argument cast in Galton’s clothes.[47] George then offered the example of the horn-length of cattle, noting that ‘my father considers a like argument as applicable to the variations of any organs of any species in size, weight, colour, capacity for performing a function, &c’. With reference to natural selection, emphasis was given to the continuity in any tendency to change over numerous generations. At the time his father wrote to *Nature*, George Darwin reported, there were no data to support the hypothesis of a link between species separation and a departure from the normal distribution, his father making ‘hypothetical remarks solely for the sake of calling attention to the subject’.[48] However, it was now something ‘my father intends to put to the test of experiment’, in the hope of demonstrating a tendency towards diminution; in the case of some cirripedes, even to the point of redundancy.[49]

In the letters sent by George Darwin to his father and to *Nature*, the arguments for the ultimate restoration of the law of Quetelet are very similar. The contrast lies not in the texts of the letters, but in the use of diagrams in the critique and their omission from the published letter. Certainly, it would have taken George some time to prepare diagrams suitable for publication — time that was not available if his father’s arguments needed buttressing at the earliest opportunity. In any case, precisely three weeks after Charles Darwin’s letter appeared in *Nature* to suggest a link between species separation and a departure from the law of Quetelet, George Darwin’s elucidatory letter was published in the same journal. Carefully crafted, but lacking the diagrams that appeared in his correspondence with his father, George Darwin gave a more detailed picture of the effects on the statistical distribution of the variation in characters arising from species separation. The departure from the normal curve, suggested by his father, was temporary. Over many, many generations the distribution would lose and regain its symmetry time and time again.

The Concurrence of Romanes

This cyclic pattern was also argued for by Charles Darwin’s eager acolyte, George Romanes (1848-1894), though for different reasons. In the spring of 1874, Romanes wrote two letters to *Nature* announcing his adherence to the theory of evolution and suggesting extensions to the arguments on rudimentary organs.[50] In the *Origin of Species* and in *Variation of Animals and Plants under Domestication*, Charles Darwin had mentioned three causes of the degeneration of useless structures: selection, disuse and economy of growth. Romanes considered the ‘dwarfing influence of impoverished conditions … by means of free intercrossing’, which the Darwins invoked in their letters to *Nature* to constitute a fourth cause.[51] He actually believed that even the four causes are insufficient to explain all cases of degeneration and that the first three causes are confounded, because:

> Selection may be considered as applying only to those rare instances in which changed conditions of life may be supposed to have rendered a previously useless organ injurious; for so far as selection operates in obliterating a useless organ, it will be more convenient, for the sake of brevity, to identify it with the Economy of Growth. Since, however, it is obvious that an injurious organ must pass through the merely useless stage before it becomes wholly suppressed, we may dismiss this case without further comment.[52]

Without invoking the concept of exponential decay as such, he further claimed that the action of economy of growth in reducing the size of a useless structure falls away in that manner:

> Suppose an organ to become suddenly useless, this principle would at first cause its rapid reduction. In proportion, however, as its presence ceases to be injurious, the arresting process becomes slower

> and slower, until a point is reached at which it is presumably *nil*. That such a point of rest must somewhere be attained seems evident, if we consider that the smaller the diminishing organ becomes the less is it subject to the influence of the Economy of Growth. In other words, when an organ undergoing reduction becomes so minute relatively to the size of the animal (or, more correctly, to the available store of nutrition), that the supply of nourishment it requires is no longer perceived by the organism at large, it then remains permanently at that size.[53]

In the second letter, Romanes described in a general way the effects on the distribution of variation. He claimed that what he was about to propose was 'suggested to me by the penetrating theory proposed by Mr. Darwin, to which, indeed, it is but a supplement'.[54] He took 'the exact converse of Mr. George Darwin's illustration', whereby a selective influence ceases because of an improvement in the conditions of life, such as food once more becoming plentiful.[55] With no need to fight over the lush pasture, the longer-horned cattle would not now enjoy an advantage over the shorter-horned, breaking the causal link between horn length and fecundity. If the average length of horn were, say 100, at the cessation (and hence reversal) of the influence, natural selection would

> rigidly eliminate the variations 101, 102, 103, &c., and favour the variations 99, 98, 97, &c. For the sake of definition we shall neglect the influence of Economy acting below 100, and so isolate the effects due to the mere withdrawal of Selection. By the condition of our assumption, all variations above 100 are eliminated, while below 100 indiscriminate variation is permitted … Now there is … a much greater chance of variations being perpetuated at or below 99, than at or above 100; for at 100 the hard line of Selection (or Economy) is fixed, while there is no corresponding line below 100. The consequence of free intercrossing would therefore be to reduce the average from 100 to 99. Simultaneously, however, with this reducing process, other variations would be surviving below 99, in greater numbers than above 99 …[56]

This imbalance would not stop the average falling still further but the tendency to fall would be countered by the greater variation amongst the shorter-horned. He continued:

> It is evident … that the more the average is reduced by this process of indiscriminate variation, the less chance there remains for its further reduction … [T]heoretically the average would continue to diminish at a slower and slower rate, until it comes to 50, where the chances in favour of increase and diminution being equal, it would remain stationary.[57]

Quoting directly from George Darwin's letter, Romanes also concluded that 'there would thus be "two operations going on side by side—the one ever destroying the distribution" round the average, "and the other ever tending to restore it".[58]

For someone so preoccupied with the use of the law of error as the distribution of variation, Galton remained noticeably silent throughout the discussion in *Nature*. There is nothing in his correspondence or published papers to provide direct evidence that he followed it at all over the winter of 1873-1874.

Later, in a letter to Charles Darwin in the summer of 1877, Romanes would write:

> I have deferred answering your letter until having had a talk with Mr. Galton about rudimentary organs. He thinks with me that if the normal size of a useful organ is maintained in a species, when natural selection is removed, the average size will tend to become progressively reduced by inter-crossing, and this down to whatever extent economy of growth remains operative in placing a premium on variations below the average at any given stage in the history of reduction.[59]

So Galton was reported to be sympathetic towards Romanes' argument, and indeed, there would appear to be some parallels between the two, in that to Galton differential birth rates across the social strata suppress natural selection and drive the physical and intellectual powers of the nation downwards.

Conclusion

It is useful at this point to compare the positions of Galton, the Darwins and Romanes on the distribution of variation in the mid-1870s. From Quetelet, Galton had taken as undeniable the fact that physical characters are normally distributed, under ordinary conditions of life. He had argued by analogy that mental abilities are also normally distributed under those same conditions. But no such ordinary conditions held in English society because of the differential in birth rates across the social strata. The result was a loss of symmetry in the distribution of attainments and hence in the distribution of abilities. Since the distribution of physical and mental attributes was also one and the same, according to Galton's free use of analogy, it may be assumed that the distribution of physical attributes also lost its symmetry under these social pressures. The distribution was skewed to the left; that is, towards the lower measures (or as Pearson would later say, positively skewed). Restoration of the symmetry could be brought about if those unnatural forces of society were countered and balanced by Draconian intervention.

Charles and George Darwin assumed that physical characters are normally distributed under ordinary conditions of life, perhaps following Quetelet to some extent, but certainly following Galton. Their interests lay in attempting to understand the effects of natural selection on the distribution when the conditions of life become unfavourable for a species. Pressed for food the species would not waste its resources by building up characters that are not essential for survival. The distribution of these characters thus becomes skewed to the left and its mean displaced towards smaller values. Although the mean would not regain its magnitude the symmetry of the distribution would be restored.[60]

Romanes also considered the distribution of physical characters at or around the point at which species separate but from the opposite perspective of a selective force, having acted, then ceasing to do so. The diminution of an unessential character, effecting a reduction in the mean magnitude and a loss of symmetry, is checked by another force, economy of growth, which slows the fall in the mean value to nought, whilst again restoring the symmetry. This appeared to Galton to be perfectly reasonable. Indeed, except for the failure of Romanes' model to re-establish the mean magnitude, there are similarities with the perceived effects of Galton's eugenic programme, which was, itself, a check on the vagaries of the social physics of Victorian England.

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1 Francis Galton, *Hereditary Genius* Macmillan, 1869; 2nd Edition (1892), 343.

2 Francis Galton, 'Hereditary Improvement', *Fraser's Magazine* 7 (1873), 116-130, 118.

3 Ibid., 120.

4 Ibid., 121.

5 Ibid.

6 Herbert Spencer, *The Principles of Biology* (London and Edinburgh: Williams and Norgate. Vol. 1, 1864; vol. 2, 1867).

7 Francis Galton, 'The First Steps Towards the Domestication of Animals'. *Transactions of the Ethnological Society of London* 3 (1865), 122-138. Charles Darwin, *The Variation of Animals and Plants under Domestication*, 2 vols (London: John Murray, 1868). Galton, 'On Blood-relationship', *Proceedings of the Royal Society* 20 (13 June 1872), 394-402; reprinted *Nature* 6 (27 June 1872), 173-176.

8 Francis Galton, 'A Theory of Heredity', *Journal of the Anthropological Institute of Great Britain and Ireland* 5 (1876), 329-348, 331.

9 Christopher B. Pritchard, *The Normal Curve of Evolutionary Biology, 1869-1877, with Special Reference to the Support Given to Francis Galton by George Darwin*, PhD Thesis, Open University, May 2005.

10 Sherrie L. Lyons, 'The Origins of T. H. Huxley's Saltationism: History in Darwin's Shadow', *Journal of the History of Biology* 28, 3 (1995), 463-494.

11 Francis Galton, *Hereditary Genius* Macmillan, 1869; edition of 1892, pp. 354-355.

12 Francis Galton, *Natural Inheritance* (London: Macmillan, 1889), 27.

13 Ibid., 27-30.

14 The specimen was found at Lowe's Harbour in January 1835. The subclass *Cirripedia* encompasses some thousand species. The vast majority are barnacles, falling into two main groups: sessile (stalkless or goose) and pedunculated (stalked or acorn). The Chonos barnacle was originally called *Arthrobalanus* by Darwin but later renamed by him *Cryptophialus minutus*. It was parasitic upon the gastropod, *Concholepas*.

15 Charles Darwin, *A Monograph of the Sub-Class Cirripedia*. *Vol. 1, Lepadidæ* (London: Ray Society, 1851); *Vol. 2, Baladinæ, Verrucidæ etc* (London: Ray Society, 1854). Idem, *A Monograph of the Fossil Lepadidæ*

(London: Palæontographical Society, 1851). *A Monograph of the Fossil Baladinæ and Verrucidæ* (London: Palæontographical Society, 1854).

16 Charles Darwin, Letter to (Johannes) Japetus Smith Steenstrup, 1 September 1850 in Charles Darwin, *Correspondence*, vol. 4, 352. Steenstrup was Denmark's leading researcher in natural history.

17 Charles Darwin, *Origin of Species*, 147-148.

18 *Variation of Animals and Plants under Domestication* runs to 900 pages and took Darwin six years to write. Meanwhile, the material which he had gathered on variation in nature was so voluminous, he abandoned plans to write the companion volume.

19 On the subject of Darwin as statistician, the views of family members, of Galton and of Pearson are discussed by Eileen Magnello, 'Karl Pearson: Evolutionary Biology and the Emergence of a Modern Theory of Statistics (1884-1936)', DPhil thesis, University of Oxford, 1993; 121-123.

20 'Review of Quetelet's *On Man*', *Athenæum* 406 (8 August 1835), 593-595; 407 (15 August 1835), 611-623; 409 (29 August 1835), 658-661. Schweber argued that this review was written by George Richardson Porter (1792-1852). Porter was the inaugural head of the statistical department of the Board of Trade from 1832 and active in both the Statistical Society of London, established in 1834, and Section F of the British Association. Schweber noted that Porter frequently corresponded with Quetelet and was 'in total command of all the material in Quetelet's book'.

21 Silvan S. Schweber, 'The Origin of the *Origin* Revisited', 283.

22 [John Herschel], 'Quetelet on Probabilities', *Edinburgh Review* 92 (1850), 1-57.

23 William Spottiswoode, 'On Typical Mountain Ranges', *Journal of the Royal Geographical Society*, 31 (1861), 149-154.

24 Francis Galton, *Hereditary Genius* (London: Macmillan, 1869).

25 Charles Darwin, Letter to Francis Galton, 23 December 1869, UCL Galton Archive 39. Emma Darwin regularly read works of fiction aloud to her husband. This practice clearly extended on occasion to philosophical and scientific works.

26 Charles Darwin, 'On the Males and Complemental Males of Certain Cirripedes, and on Rudimentary Structure', *Nature* 8 (25 September 1873), 431-432. Gerd Gigerenzer and his co-writers were wrong to claim that 'Darwin himself never considered the applicability (or inapplicability) of the law of errors to variation'. See Gerd Gigerezer *et al*, *The Empire of Chance: How Probability Changed Science and Everyday Life* (Cambridge University Press, 1989), 143.

27 George Darwin, 'Variations of Organs', *Nature* 8 (16 October 1873), 505.

28 George Romanes, 'Natural Selection and Dysteleology', *Nature* 9 (12 March 1874), 361-362; idem, 'Rudimentary Organs', *Nature* 9 (9 April 1874), 440-441.

29 M. Eileen Magnello, 'Karl Pearson's Gresham Lectures: W. F. R. Weldon, Speciation and the Origins of Pearsonian Statistics', *British Journal of the History of Science* 29 (1996), 43-63. Walter Frank Raphael Weldon (1860-1906) and Karl Pearson were the first biometricians proper.

30 Christopher B. Pritchard, *The Normal Curve of Evolutionary Biology, 1869-1877, with Special Reference to the Support Given to Francis Galton by George Darwin*, PhD Thesis, Open University, May 2005; chapter 5.

31 Charles Wyville Thomson, 'Notes from the Challenger. VI', *Nature* 8 (28 August 1873), 347-349. The studies undertaken by Thomson on the 1872-76 voyages of *H. M. S. Challenger* refuted the hypothesis of a constant sea temperature at great depth and discovered new species at depths near three thousand fathoms.

32 Charles Darwin, 'On the Males and Complemental Males of Certain Cirripedes', 432.

33 Ibid.

34 George Howard Darwin, Letter to Charles Darwin, undated but written between 25 September and 3 October 1873, Cambridge University Library DAR 205.1.

35 According to Warwick, 'Routh was by far the most successful of all Cambridge coaches and was probably the most influential mathematics teacher of all time'. See Andrew Warwick, *Masters of Theory*, 231.

36 For details of the other two, see Pritchard, PhD Thesis, 143-145.

37 Charles Darwin, *Variations of Animals and Plants under Domestication*, vol. 2, 158 *ff*. Alfred Russel Wallace, Letter to Charles Darwin, February 1868, in *More Letters of Charles Darwin*, edited by Francis Darwin & A. C. Seward (London: John Murray, 1903), vol. 1, 288. The letter is probably from late in the month.

38 Alfred Russel Wallace, Letter to Charles Darwin, 1 March 1868, *More Letters*, vol. 1, 291.

39 Charles Darwin, Letter to Alfred Russel Wallace, 17 March 1868, British Library, Add. 46434. Hereinafter, the British Library is denoted BL.

40 Ibid.

[41] Alfred Russel Wallace, Letter to Charles Darwin, together with George Darwin's appended notes, 24 March 1868, Cambridge University Library DAR. 106: B61-62 & B158-163. Charles Darwin's subsequent comments are to be found in a letter to Wallace of 6 April 1868, BL Add. 46434.

[42] George Darwin, Letter to Charles Darwin, undated but written between 25 September and 3 October 1873, Cambridge University Library DAR 205.1.

[43] Ibid.

[44] Ibid.

[45] George Howard Darwin, Letter to Charles Darwin, 3 October 1873, Cambridge University Library DAR. 210.2.

[46] Charles Darwin, Letter to George Howard Darwin, 3 October 1873, Cambridge University Library DAR. 210.1. Charles Darwin wrote that 'I s[houl]d not like to publish even a son's letter as my own'.

[47] Francis Galton, *Hereditary Genius*, 24.

[48] Charles Darwin, 'On the Males and Complemental Males of Certain Cirripedes', 432.

[49] Ibid. No such experiments were carried out.

[50] George Romanes met Darwin for the first time in the summer of 1874 and being a contemporary of Darwin's children — he was the same age as Francis Darwin — he fitted in well at Down. Romanes' letters to *Nature* found favour with Darwin. The detail is in a flurry of letters of July 1874 (Cambridge University Library, DAR 52, ser.4:1-2; DAR 52:8-9; DAR 52, ser.4:7). As a physiologist, Romanes had worked with Hooker at Kew and had carried out seminal work on jellyfish at a small laboratory on the Scottish coast.

[51] George Romanes, 'Natural Selection and Dysteleology', *Nature* 9 (12 March 1874), 361-362. The term 'dysteleology', used by Romanes on p. 361 to describe the fourth cause, was Ernst Haeckel's word for 'purposelessness'.

[52] Ibid., 361.

[53] Ibid., 362.

[54] George Romanes, 'Rudimentary Organs', *Nature* 9 (9 April 1874), 440-441; 440.

[55] Ibid.

[56] Ibid., 440-441.

[57] Ibid., 441.

[58] Ibid.

[59] Ethel D. Romanes (ed.), *The Life and Letters of George John Romanes*, 2nd edition (London: Longman, Green 1896), 56-57.

[60] In the early 1890s, Karl Pearson and W. F. R. Weldon explored the association between speciation under the Darwinian hypothesis and skew distributions of characters. Pearson assumed that normal curves afford evidence of evolutionary stability, both in his Gresham lectures and in a paper submitted to the Royal Society. Interestingly, the paper was refereed by George Darwin, who asked Pearson for biological evidence for his assumption. George Darwin, Referee's Report, dated 9 November 1893, Royal Society Archive, RR 12.11. See Theodore M. Porter, *The Scientific Life in a Statistical Age* (Princeton University Press, 2004), 238.