



The Development of Francis Galton's Ideas on the Mechanism of Heredity

MICHAEL BULMER

The Old Vicarage
Chittlehampton
Umberleigh EX37 9RQ
U.K.

Abstract. Galton greeted Darwin's theory of pangenesis with enthusiasm, and tried to test the assumption that the hereditary particles circulate in the blood by transfusion experiments on rabbits. The failure of these experiments led him to reject this assumption, and in the 1870s he developed an alternative theory of heredity, which incorporated those parts of Darwin's theory that did not involve the transportation of hereditary particles throughout the system. He supposed that the fertilized ovum contains a large number of hereditary elements, which he collectively called the "stirp," a few of which are patent, developing into particular cell types, while the rest remain latent; the latent elements can be transmitted to the next generation, while the patent elements, with rare exceptions, cannot since they have developed into cells.

The problem with this theory is that it does not explain the similarity between parent and child unless there is a high correlation between latent and patent elements. Galton probably came to realize this problem during his subsequent statistical work on heredity, and he quietly dropped the idea that patent elements are not transmitted in *Natural Inheritance* (1889).

Galton thought that brothers and sisters had identical stirps, and he attributed differences between them to variability in the choice of patent elements from the stirp, that is to say to developmental variability. He attributed the likeness of monozygotic twins to the similarity of their developmental environment. Galton's twin method was to track the life history changes of twins to see whether twins who were similar at birth diverged in dissimilar environments or whether twins who were dissimilar at birth converged in similar environments. It is quite different from the modern twin method of comparing the similarities between monozygotic and dizygotic twins, on the assumption that monozygotic twins are genetically identical whereas dizygotic twins are not.

It has been argued that Galton foreshadowed Weismann's theory of the continuity of the germ-plasm, but this is only true in a weak sense. They both believed that the inheritance of acquired characters was either rare or impossible, but Galton did not forestall the essential part of Weismann's theory, that the germ-plasm of the zygote is doubled, with one part being reserved for the formation of the germ-cells.

Keywords: Galton, heredity, pangenesis, stirp, twins, Weismann, continuity of the germ-plasm

It has recently been argued that the reconciliation of the hypothesis of natural selection with the facts and theory of heredity was the major challenge faced

by Darwinism during its first sixty years.¹ This culminated in the synthesis of Darwinism, Mendelism, and biometry which led to theoretical population genetics and the modern synthesis, but historical understanding of how this happened requires consideration of pre-Mendelian theories of heredity in the nineteenth century.² The work of Francis Galton (1822–1911) is of particular importance in this context.

Galton's ideas about heredity fell into three phases: (1) his attempt to demonstrate the inheritance of human mental abilities, in particular in *Hereditary Genius* (1869), and to distinguish between the effects of nature and nurture in the history of twins,³ (2) his experiments on pangenesis and his physiological theory of heredity in the 1870s,⁴ and (3) his subsequent construction of a purely statistical theory of heredity, leading to the techniques of regression and correlation and to the law of ancestral heredity.⁵

His work in the first and third of these phases is well-known, and the latter in particular has been thoroughly reviewed.⁶ In this paper I shall analyze his work in the second phase, on the physiological mechanism of heredity. It is less well-known than his other work, but is equally important for understanding the problems faced by nineteenth-century biologists in constructing a theory of heredity to underpin the Darwinian hypothesis of natural selection. It also throws light on the rationale behind his method of studying the history of twins to distinguish between nature and nurture, as well as on his biological interpretation of regression and of the law of ancestral heredity.

¹ Jean Gayon, *Darwinism's Struggle for Survival: Heredity and the Hypothesis of Natural Selection* (Cambridge: Cambridge University Press, 1998).

² See Gayon (above); Robert Olby, *Origins of Mendelism*, 2nd edn. (Chicago: University of Chicago Press, 1985); William B. Provine, *The Origins of Theoretical Population Genetics* (Chicago: University of Chicago Press, 1971).

³ Francis Galton, "Hereditary Talent and Character," *Macmillan's Mag.*, 12 (1865), 157–166, 318–327; *Hereditary Genius* (London: Macmillan, 1869), reprinted with an introduction by H. J. Eysenck (London: Friedmann, 1979); "The History of Twins, as a Criterion of the Relative Powers of Nature and Nurture," *J. Anthropol. Inst.*, 5 (1875), 391–406.

⁴ Francis Galton, "Experiments in Pangenesis, by Breeding from Rabbits of a Pure Variety, into whose Circulation Blood Taken from other Varieties had Previously Been Largely Transfused," *Proc. Roy. Soc.*, 19 (1871), 393–410; "On Blood Relationship," *Proc. Roy. Soc.*, 20 (1872), 394–402; "A Theory of Heredity," *J. Anthropol. Inst.*, 5 (1875), 329–348.

⁵ Francis Galton, "Typical Laws of Heredity," *Proc. Roy. Inst.*, 8 (1877), 282–301; "Regression Towards Mediocrity in Hereditary Stature," *J. Anthropol. Inst.*, 15 (1885), 246–263; *Natural Inheritance* (London: Macmillan, 1889); "The Average Contribution of each Several Ancestor to the Total Heritage of the Offspring," *Proc. Roy. Soc.*, 61 (1897), 401–413.

⁶ As well as the references in note 2, see Stephen M. Stigler, *The History of Statistics: The Measurement of Uncertainty Before 1900* (Cambridge, Mass.: Harvard University Press, 1986), chap. 8; M. Eileen Magnello, "Karl Pearson's Mathematization of Inheritance: From Ancestral Heredity to Mendelian Genetics," *Ann. Sci.*, 55 (1998), 35–94; Michael Bulmer, "Galton's Law of Ancestral Heredity," *Heredity*, 81 (1998), 579–585.

Galton's thoughts about the mechanism of heredity were stimulated by the publication of Darwin's theory of pangenesis in 1868.⁷ Darwin supposed that cells throw off minute "gemmules," which circulate throughout the system; each type of cell produces a different type of gemmule, which can develop into a cell like that from which it was derived. Gemmules are collected in germ cells for transmission to future generations; to explain reversion, whereby an individual may inherit characters present in more remote ancestors but not expressed in either of the parents, Darwin supposed that gemmules may be transmitted in a latent state.

Galton's enthusiastic reception of this theory is demonstrated in the final section of *Hereditary Genius*, and he tried to verify it by transfusing blood between different varieties of rabbits; the negative results of these experiments led him in 1871 to reject that part of the theory which required, as he thought, the transportation of hereditary particles in the blood.

He developed his own theory, based largely on the other parts of Darwin's work, and published it in two papers, the first in 1872 and the second in 1875. In the latter paper, he coined the name "stirp" for the sum-total of gemmules in the newly-fertilized ovum. He supposed that a few of these gemmules were developed into the cells of the adult, the residue remaining latent. Having rejected (except as a rare exception) Darwin's idea that cells throw off gemmules that are collected in the germ cells, he supposed that the germ cells contributing to the next generation predominantly comprised the latent residue of gemmules in the stirp. He did not appreciate the difficulty of accounting for the correlation between parent and offspring under this model.

After 1875 he turned his attention to developing a statistical rather than a physiological theory of heredity. This work, in particular the law of ancestral heredity, led him to suppose that latent and patent gemmules were equally frequent and had the same chance of being transmitted to the next generation. He briefly discussed this idea, under which the correlation between parent and offspring can be explained much more easily, in *Natural Inheritance* (1889), though he did not acknowledge the change from his previous theory.

The purpose of this paper is to describe and analyze the development of Galton's ideas about the mechanism of heredity, comparing them with Darwin's theory of pangenesis, from which some of them originated, and with Weismann's ideas on heredity, which others of them partially anticipated. Emphasis is placed on the role of internal factors in the development of Galton's ideas, rather than on his socio-economic environment and

⁷ Charles Darwin, *The Variation of Animals and Plants under Domestication* (London: John Murray, 1868). Quotations are from the second edition (1875), reprinted 1905.

his interest in eugenics, which have been stressed by others.⁸ I begin by discussing his knowledge of the laws of heredity when he published “Hereditary talent and character” in 1865, prior to the publication of Darwin’s theory of pangenesis.

Galton’s Knowledge of Heredity in 1865

In “Hereditary talent and character,” Galton’s main aim was to demonstrate the fact of the inheritance of human mental qualities. For example, from a select biographical list of 605 notable persons who lived between 1453 and 1853, he extracted 330 names distinguished in literature or science and found that 51 of them, or 1 in 6, had a first degree relative of literary distinction in this sublist; he estimated that there may have been one million educated men in Europe during that period, of whom 330, or only 1 in 3000, achieved literary distinction. By restricting his attention to the open professions of literature and science, as contrasted with the more closed professions of statesmanship and generalship, he argued that he had excluded the effect of social position and had isolated the effect of heredity in this calculation.

Thus Galton claimed that a large hereditary component was involved in achieving literary or scientific distinction. Although his argument for excluding social factors was naive, he acknowledged “our ignorance of the laws which govern the inheritance even of physical features.” He mentions three sources for the information available to him on this subject: *Traité de l’Hérédité Naturelle* by Prosper Lucas, *The Physiology of Common Life* by G. H. Lewes, and Charles Darwin’s *Origin of Species*;⁹ and he recognizes three principles that will be important in all his future work: biparental inheritance, reversion to ancestral characters, and the rejection of any significant role for the inheritance of acquired characters.

The idea of biparental inheritance, that “the qualities of each individual are due to the combined influence of his two parents,”¹⁰ was acknowledged

⁸ Ruth Schwarz Cowan, “Nature and Nurture: the Interplay of Biology and Politics in the Work of Francis Galton,” *Stud. Hist. Biol.*, 1 (1977); Donald A. MacKenzie, *Statistics in Britain, 1865–1930: The Social Construction of Scientific Knowledge* (Edinburgh: Edinburgh University Press, 1981).

⁹ Prosper Lucas, *Traité philosophique et physiologique de l’hérédité naturelle dans les états de santé et de la maladie du système nerveux*, 2 vols (Paris: J. B. Baillière, 1847–1850); G. H. Lewes, *The Physiology of Common Life* (Edinburgh, 1859); Charles Darwin, *The Origin of Species by Means of Natural Selection or The Preservation of Favoured Races in the Struggle for Life* (London: John Murray, 1859).

¹⁰ Galton, “Hereditary Talent and Character” (above, n. 3), p. 158.

by all three of Galton's stated sources.¹¹ He had found in his study of the inheritance of talent that sons of distinguished fathers were likely to be more distinguished than average but less so than their fathers. He attributed the latter tendency in part to the fact that he could not take the contribution of the mother into account: "I have shown . . . that intellectual capacity is so largely transmitted by descent that, out of every hundred sons of men distinguished in the open professions, no less than eight are found to have rivalled their fathers in eminence. . . . The proportion we have arrived at takes no account whatever of one-half of the hereditary influences that form the nature of the child. My particular method of enquiry did not admit of regard being paid to the influences transmitted by the mother."¹²

Galton also applied the principle of equal parental contributions in the following passage: "The share that a man retains in the constitution of his remote descendants is inconceivably small. The father transmits, on an average, one-half of his nature, the grandfather one-fourth, the great-grandfather one-eighth; the share decreasing step by step, in a geometrical ratio, with great rapidity."¹³ The argument is straightforward, and can be put today like this. If a child inherits half its "genes" from its father (and half from its mother), and if the father inherits half of *his* "genes" from *his* father, then the child must have inherited one quarter of its "genes" from its paternal grandfather, and so on. The argument is valid under any form of biparental inheritance, whatever term is substituted for "gene." It is a restatement of the law of halving known for a long time to breeders in terms of "blood fractions"; this law is a simple consequence of biparental inheritance. The point was later made in a similar way by Weismann in 1885.¹⁴ Some confusion has

¹¹ For Lucas' *Traité*, see Frederick B. Churchill, "From heredity theory to *Vererbung*," *Isis* 78 (1987), 342; for Lewes' *Physiology of Common Life*, see Robert Olby, *Origins of Mendelism*, 2nd edn. (Chicago: University of Chicago Press, 1985), pp. 170–174.

¹² Galton, "Hereditary Talent and Character" (above, n. 3), pp. 318–319. The overwhelming majority of eminent persons in Galton's lists were men, presumably because it was very difficult in contemporary social conditions for women to demonstrate their ability by becoming eminent in the professions. For this reason, Galton was unable to determine the ability of women by his criterion of achieving professional eminence. For the same reason, he invariably referred to eminent people as men ("sons of men distinguished in the open professions").

¹³ Galton, "Hereditary Talent and Character" (above, n. 3), pp. 326–327.

¹⁴ August Weismann, "The Continuity of the Germ-Plasm as the Foundation of a Theory of Heredity"; English translation in Edward B. Poulton, Selmar Schönland, and Arthur E. Shipley, *Essays upon Heredity and Kindred Biological Problems by Dr. August Weismann* (Oxford: Clarendon Press, 1889), p. 179.

arisen from Karl Pearson's misinterpretation of the above passage as the "first enunciation of the Law of Ancestral Heredity."¹⁵

The second principle mentioned briefly in the 1865 paper is the law of reversion, whereby an individual may exhibit characters present in more remote ancestors but not expressed in either of the parents. We discussed above Galton's suggestion that one reason why sons were often less distinguished than their fathers was because the calculation considers only the influence of the father and ignores that of the mother. Immediately after the passage quoted there, he continues: "Lastly, though the talent and character of both of the parents might, in any particular case, be of a remarkably noble order, and thoroughly congenial, yet they would necessarily have such mongrel antecedents that it would be absurd to expect their children to invariably equal them in their natural endowments. The law of atavism prevents it."¹⁶ In other words, another reason for children being less distinguished than their parents was their tendency to revert to more remote ancestors, who would on average be less distinguished than very distinguished parents. (Atavism is another name for reversion.) The law of reversion was well-known in the middle of the nineteenth century, and was discussed by Prosper Lucas in his *Traité de l'Hérédité* and by Charles Darwin in the *Origin of Species*.

Galton was ahead of his time in rejecting any significant role for the inheritance of acquired characters:

Can we had anything down to our children, that we have fairly won by our own independent exertions? Will our children be born with more virtuous dispositions, if we ourselves have acquired virtuous habits? Or are we no more than passive transmitters of a nature we have received, and which we have no power to modify? There are but a few instances in which habit even seems to be inherited. The chief among these are such as those of dogs being born excellent pointers; of the attachment to man shown by dogs; and of the fear of man, rapidly learnt and established among the birds of newly-discovered islands. But all of these admit of being accounted for on other grounds than the hereditary transmission of habits. Pointing is, in some faint degree, a natural disposition of all dogs. Breeders have gradually improved upon it, and created the race we now possess. There is nothing to show that the reason why dogs are born staunch pointers is that their parents had been broken into acquiring an artificial habit. . . .

¹⁵ Karl Pearson, *The Life, Letters and Labours of Francis Galton* (Cambridge University Press, 1924), V. II, 84. See Bulmer, "Galton's Law of Ancestral Heredity" (above, n. 6) for a fuller discussion.

¹⁶ Galton, "Hereditary Talent and Character" (above, n. 3), p. 319.

If we examine the question from the opposite side, a list of life-long habits in the parents might be adduced which leave no perceptible trace on their descendants. . . . If the habits of an individual are transmitted to his descendants, it is, as Darwin says, in a very small degree, and is hardly, if at all, traceable.

We shall therefore take an approximately correct view of the origin of our life, if we consider our own embryos to have sprung immediately from those embryos whence our parents were developed, and those from the embryos of *their* parents, and so on for ever.¹⁷

The inheritance of acquired characters (the effect of use and disuse) was widely accepted from ancient times through to the nineteenth century.¹⁸ Darwin thought that use and disuse played a definite role in evolution, albeit secondary to that of natural selection. He devotes a whole section of the *Origin* to the effects of use and disuse (134–139), and in discussing the habits of the pointer dog he writes (my italics): “It may be doubted whether any one would have thought of training a dog to point, had not some one dog naturally shown a tendency in this line; and this is known occasionally to happen, as I once saw in a pure terrier. When the first tendency was once displayed, methodical selection *and the inherited effects of compulsory training* in each generation would soon complete the work.”¹⁹ Thus Darwin attributes the development of the pointing instinct partly to selection and partly to the inherited effects of training; Galton disputes the second part of this claim. Ruth Cowan has argued that Galton’s rejection of the inheritance of acquired characters was sociopolitical, being determined by his eugenic convictions,²⁰ but a simpler explanation seems equally convincing. The passage quoted above is well-argued and suggests that Galton had thought carefully about the evidence for the inheritance of acquired characters, and concluded on internal grounds that it was weak.

In conclusion, Galton recognized three principles when he wrote his first paper on heredity in 1865. The first is biparental inheritance, from which the law of halving follows. The second is the law of reversion, from which it follows that offspring of very distinguished parents are likely to be less distinguished than them. The third is the rejection of any significant role for the inheritance of acquired characters. He developed these ideas further during the next ten years, but in the meantime he was greatly influenced by Darwin’s

¹⁷ Ibid., pp. 321–322.

¹⁸ Conrad Zirkle, “The Early History of the Inheritance of Acquired Characters and of Pangenesis,” *Trans. Amer. Phil. Soc.*, 35 (1951), 95–141.

¹⁹ Darwin, *Origin of Species* (above, n. 9), p. 214.

²⁰ Cowan, “Nature and Nurture” (above, n. 8), p. 141.

“provisional hypothesis of pangenesis,” published in 1869. It is convenient to digress now to consider this hypothesis.

Darwin’s Theory of Pangenesis (1868)

The theory of pangenesis, constructed to explain the facts about inheritance and development known to Darwin, made the following assumptions: (1) The cells of the body throw off minute granules, called gemmules, “which circulate freely throughout the system”;²¹ each type of cell produces a different type of gemmule, that can be thought of as a miniature replica of itself. (2) The gemmules can multiply by self-division, and can in the right conditions develop into a cell like those from which they were originally derived. (3) The gemmules “are collected from all parts of the system to constitute the sexual elements, and their development in the next generation forms a new being; but they are likewise capable of transmission in a dormant state to future generations and may then be developed.”²²

Darwin explained the facts of development by assuming that each gemmule has an “elective affinity . . . for that particular cell which precedes it in due order of development”;²³ after attachment to that cell, the gemmule develops into its appropriate cell type. To explain how an amputated limb can be regenerated and how an organism can reproduce by budding as well as sexually, he supposed that gemmules of every variety are present in every tissue, as a consequence of their free circulation throughout the body.

The inheritance of acquired characters and of the effects of use or disuse are explained by supposing that when a cell has become structurally modified it throws off similarly modified gemmules, which will be inherited. Darwin also used the theory to explain other “facts” which are no longer believed, such as telegony, the effect of mating a male to a female on subsequent offspring of that female by other males.²⁴

The explanation of reversion will now be discussed in detail because of its importance in Galton’s theory of heredity. Reversion or atavism occurs when a child resembles a grandparent or more distant ancestor for some character not possessed by either of its parents. When two varieties are crossed, Darwin knew that, as a general rule, the “offspring in the first generation are nearly intermediate between their parents, but their grandchildren and succeeding generations continually revert, in a greater or lesser degree, to one

²¹ Darwin, *Variation of Animals and Plants* (above, n. 7), II, 456.

²² *Ibid.*, p. 457.

²³ *Ibid.*, p. 462.

²⁴ R. W. Burkhardt, “Closing the Door on Lord Morton’s Mare: The Rise and Fall of Telegony,” *Stud. Hist. Biol.*, 3 (1979), 1–21.

or both of their progenitors.”²⁵ Mendelian genetics would attribute this fact to segregation. Naudin proposed this idea in 1865, though his hypothesis fell short of Mendel’s because he believed that the hereditary elements segregate according to species or variety, without any mixing of them.²⁶ Naudin’s hypothesis of segregation was not fully accepted by Darwin because it did not explain distant reversion, in which the offspring from a cross between two races resemble a very distant ancestor. For example, Darwin showed that all races of domestic pigeons arose from the wild rock pigeon *Columba livia*, which is slaty blue in color with two black wing bars. The pure bred domestic races have lost the wild color and wing bars, but occasionally revert to the ancestral appearance, blue with two black wing bars. When two domestic races are crossed, for example a black with a white-colored race, the progeny or grandprogeny often revert to the ancestral appearance, despite the fact that the races from which they were derived have bred true for several hundred years. Darwin was greatly struck by this phenomenon, which would today be attributed to complementary gene action;²⁷ the presence of two genes is required to produce the ancestral appearance, one of which is present in the first race and the other in the second.

Darwin sought an explanation that would account both for near and for distant reversion. He assumed that only some of the gemmules inherited by the offspring develop into cells, the rest remaining dormant or latent. Consider first reversion in the grandchildren following a cross between two varieties. As a hypothetical example, later used by Darwin in correspondence with Galton, suppose that a white and a black variety of plant are crossed to produce gray offspring, the usual case in which hybrid offspring are intermediate between the parents. The offspring possess both white and black gemmules, which produce gray tissue when it develops, and this gray tissue produces gray gemmules; but the plant also possesses unmodified, dormant white and black gemmules. Thus the gonads of the hybrid contain white, gray, and black gemmules, so that when the two hybrids pair they can have white, pale gray, gray, dark gray, or black offspring. This is a modified version of Naudin’s hypothesis of segregation.²⁸

Hybrids are not always intermediate between the two parental forms but may resemble one of them in a particular character. Darwin calls this form prepotent in the transmission of the character (we should today call the character dominant), and explains it by “assuming that the one form has some

²⁵ Darwin, *Variation of Animals and Plants* (above, n. 7), II, 28.

²⁶ Olby, *Origins of Mendelism* (above, n. 2), pp. 47–54.

²⁷ William Bateson, *Mendel’s Principles of Heredity* (Cambridge University Press, 1909).

²⁸ Darwin, *Variation of Animals and Plants* (above, n. 7), II, 486–87.

advantage over the other in the number, vigour, or affinity of its gemmules.”²⁹ For example, there are two shapes of flower in the snapdragon *Antirrhinum majus*, the normal, irregular shape and the peloric, regular shape. Darwin crossed normal with peloric plants and all the offspring were normal, whether the cross was of normal pollen with a peloric mother plant or the reciprocal. Darwin allowed these hybrid offspring to sow themselves, “and out of a hundred and twenty-seven seedlings, eighty-eight proved to be common snapdragons, two were in an intermediate condition between the peloric and normal state, and thirty-seven were perfectly peloric, having reverted to the structure of their one grandparent.”³⁰ Today this is regarded as a classic example of Mendelian inheritance for a dominant gene, but Darwin’s explanation was different. He supposed that the tendency to produce the normal character prevailed in the first generation because of the advantage of normal over peloric gemmules; but that the tendency to produce pelorism had gained in strength by the intermission of a generation because the dormant peloric gemmules had increased in number relative to the normal gemmules, since the latter had been used up in producing normal flowers. He attributes to the same cause the “fact” that certain diseases regularly appear in alternate generations.

Distant reversion in crosses is explained in a rather similar way. When a black domestic pigeon is crossed with a white pigeon, the progeny will only have half the number of the black or white gemmules present in the respective parent. This may not be enough to allow the development of either of these characters, leaving it open for the dormant blue gemmules inherited from both parents to develop, causing reversion to the ancestral rock-pigeon color.

Galton’s Reaction to Pangenesis

Galton read Darwin’s *Variation of Animals and Plants under Domestication* with great interest. His copy of the book in the Galton Archives is extensively annotated, particularly the chapters on “Inheritance” and “Pangenesis.”³¹ His pencil notes indicate that he reacted favorably to the theory of pangenesis, although he had reservations about the inheritance of acquired characters, and he incorporated a discussion of the theory at the end of *Hereditary Genius*, with the enthusiastic introduction: “This theory . . . is – whether it be true or not – of enormous service to those who enquire into heredity. It gives a key that unlocks every one of the hitherto unopened barriers to our comprehension

²⁹ Ibid., p. 471.

³⁰ Ibid., pp. 56–57.

³¹ Cowan, “Nature and Nurture” (above, n. 8), p. 167.

of its nature.” This theory . . . is – whether it be true or not – of enormous service to those who enquire into heredity. It gives a key that unlocks every one of the hitherto unopened barriers to our comprehension of its nature.”³² I shall describe his use of metaphor to illustrate the theory of pangenesis in *Hereditary Genius*, before turning to his attempt to verify the theory of pangenesis experimentally.

Galton likened the way in which development of the body occurs through the tendency of gemmules to attach themselves to particular cells, to the development of human assemblages through the free interaction of individual men. He took the development of a watering-place as an example, starting from a few houses which were rented by holiday folk, who raised a demand for further accommodation, which in turn led to the development of shops and an inn, and so on.

He used the same metaphor to introduce latent gemmules as an explanation of reversion:

I will continue to employ the same metaphor, to explain the manner in which apparent sports of nature are produced, such as the sudden appearance of a man of great abilities in undistinguished families. Mr. Darwin maintains, in the theory of Pangenesis, that the gemmules of innumerable qualities, derived from ancestral sources, circulate in the blood and propagate themselves, generation after generation, still in the state of gemmules, but fail in developing themselves into cells, because other antagonistic gemmules are prepotent and overmaster them, in the struggle for points of attachment. Hence there is a vastly larger number of capabilities in every living being, than ever find expression, and for every *patent* element there are countless *latent* ones. The character of a man is wholly formed through those gemmules that have succeeded in attaching themselves; the remainder that have been overpowered by their antagonists, count for nothing; just as the policy of a democracy is formed by that of the majority of its citizens, or as the parliamentary voice of any place is determined by the dominant political views of the electors: in both instances, the dissentient minority is powerless . . .

Suppose that by some alteration in the system of representation, two boroughs, each containing an Irish element in a large minority, the one having always returned a Whig and the other a Conservative, to be combined into a single borough returning one member. It is clear that the Whig and Conservative party will neutralize one another, and that the union of the two Irish minorities will form a strong majority, and that a member professing Irish interests is sure to be returned. This strictly

³² Galton, *Hereditary Genius* (above, n. 3), p. 364.

corresponds to the case where the son has marked peculiarities, which neither of his parents possessed in a patent form.³³

Galton assumes that the gemmules “circulate in the blood.” He also infers that there are far more latent than patent elements because “there is a vastly larger number of capabilities in every living being, than ever find expression.” He then uses a political metaphor to explain reversion under the theory of pangenesis; he has translated Darwin’s explanation of distant reversion in pigeons into human terms by equating Whigs to a black race of pigeon, Conservatives to a white race, and the Irish to the ancestral blue rock-pigeon. (Compare the final paragraph of the previous section.) He concludes rather optimistically that “these similes . . . give considerable precision to our views on heredity.”³⁴

Galton also sketched in rough outline how he thought a mathematical theory of heredity based on the theory of pangenesis might be formulated, but his suggestions for developing the theory were vague and his proposal was still-born.

We turn to Galton’s experiments on pangenesis. He assumed that Darwin’s gemmules “circulate in the blood and propagate themselves” (see quotation above), and that “they swarm in the blood . . . and circulate freely with it”,³⁵ though Darwin had said only that they “circulate freely throughout the system.” He therefore devised a careful series of experiments to test the theory of pangenesis by transfusing blood between different varieties of rabbits. They were carried out at the London Zoo between 1869 and 1871, the Prosector of the Zoo making the operations with Galton’s assistance. Galton summarized his aims and conclusions as follows:

It occurred to me . . . that the truth of Pangenesis admitted of a direct and certain test. I knew that the operation of transfusion of blood had been frequently practised with success on men as well as animals, and that it was not a cruel operation . . . I therefore determined to inject alien blood into the circulation of pure varieties of animals (of course, under the influence of anaesthetics), and to breed from them, and to note whether their offspring did or did not show signs of mongrelism. If Pangenesis were true, according to the interpretation which I have put upon it, the results would be startling in their novelty, and of no small practical use; for it

³³ Ibid., pp. 367–386.

³⁴ Ibid., p. 368. For Galton’s use of analogies see Gerd Gigerenzer, et al. *The Empire of Chance* (Cambridge: Cambridge University Press, 1989), pp. 55–57; J. S. Wilkie, “Galton’s Contribution to the Theory of Evolution with Special Reference to his Use of Models and Metaphors,” *Ann. Sci.*, 11, 194–205.

³⁵ Galton, “Experiments in Pangenesis” (above, n. 4), p. 394.

would become possible to modify varieties of animals, by introducing dashes of new blood, in ways important to breeders. Thus, supposing a small infusion of bull-dog blood was wanted in a breed of greyhounds, this, or any more complicated admixture, might be effected (possibly by operating through the umbilical cord of a newly born animal) in a single generation.

I have now made experiments of transfusion and cross circulation on a large scale in rabbits, and have arrived at definite results, negating, in my opinion, beyond all doubt, the truth of the doctrine of Pangenesis.³⁶

Two types of experiment were performed. In the first, defibrinized blood from a common lop-eared rabbit was injected into a silver-gray rabbit; common rabbits of different colors (yellow, common gray, and black and white) were used. The transfused silver-gray rabbits were allowed to breed, and out of 36 offspring, 35 were silver-gray and one was silver-gray with a white foot. Galton writes: "This white leg gave me great hopes that Pangenesis would turn out to be true, though it might easily be accounted for by other causes."³⁷ He also found that some of the does were sterile when wholly rather than partially defibrinized blood was used, and he wondered if the general failure of the experiments to lead to mongrelism was due to the gemmules being removed with the fibrin.

He therefore did a second type of experiment in which a cross circulation was established between the carotid arteries of a common rabbit and a silver-gray rabbit, the transfused rabbits being allowed to breed with their own kind. Out of 50 offspring of transfused silver-gray rabbits, 49 were silver-gray and one was Himalayan (sandy with black tips); Galton's stock of silver-gray rabbits was known to throw the occasional Himalayan in the absence of treatment, so that this could not be attributed to the transfusion. Out of 38 offspring of transfused common rabbits, all were like their parents and none was silver-gray.

Galton concluded that the doctrine of pangenesis, as he had interpreted it, was pure and simple, incorrect. He considered two alternative hypothesis: (1) the reproductive elements reside in the gonads, "whence they are set free by an ordinary process of growth, the blood merely supplying nutriment to that growth"; (2) "they reside in the blood itself," being derived from somatic cells and transported to the gonads. Galton distinguished between two variants of the second hypothesis: (2a) the reproductive elements are independent residents in the blood; (2b) they are only temporary residents in it, being "continually renewed by fresh arrivals from the framework of the

³⁶ *Ibid.*, p. 395.

³⁷ *Ibid.*, p. 402.

body.” He identified (2a) with Darwinian pangenesis, which his experiments had disproved, but points out that they prove nothing against (2b) since “in this latter case, the transfused gemmules would have perished, just like the blood-corpuscles, long before the period had elapsed when the animals had recovered from their operations.” He urges that experiments should be done to test this possibility by trying “to get the male rabbits to couple immediately, and on successive days, after they have been operated on.”

Galton asked Darwin’s advice about these experiments and kept him informed of their progress. It is clear from the surviving correspondence,³⁸ as well as from the quotation above, that both men were hoping for the results to be positive. Thus Mrs Darwin wrote to her daughter: “F. Galton’s experiments about rabbits (viz. injecting black rabbit’s blood into grey and *vice versa*) are failing, which is a dreadful disappointment to them both”; and Galton wrote to Darwin: “Good rabbit news! One of the litters has a white forefoot.” (This was the case mentioned above. Pearson remarks that the appearance of a white forefoot is a common event, and notes that Galton seized any feature he could that supported mongrelization and hence demonstrated pangenesis.)

It is also clear that Darwin knew the nature of the experiments and did nothing to discourage them. However, when he read Galton’s paper he sent a rebuttal to *Nature*,³⁹ pointing out that his theory of pangenesis did not presuppose the circulation of gemmules in the blood, and adding that when he first heard of Galton’s experiments, he did not reflect sufficiently on the subject and had not seen the difficulty of believing in the presence of gemmules in the blood. Galton took this rebuttal in good part.⁴⁰ The friendship between the two men remained unbroken, and Darwin even took a more active role in the blood transfusion experiments, which went on for some time, by housing and breeding from some of the rabbits at Down House. The results of these further experiments were negative, but they were never published; it is not known whether they were intended to test the theory that the gemmules are temporary residents in the blood under hypothesis (2b) above, but Galton’s subsequent theories assumed this process to be of minor importance, if it existed at all.

Galton’s Theory of Heredity in the 1870s

Having rejected Darwin’s theory of pangenesis, Galton set to work to develop an alternative theory, in which he incorporated those parts of Darwin’s theory

³⁸ Pearson, *Life of Galton* (above, n. 15), II, chap. 10.

³⁹ Charles Darwin, “Pangenesis,” *Nature*, 3 (1871), 502–503.

⁴⁰ Francis Galton, “Pangenesis,” *Nature*, 4 (1871), 5–6.

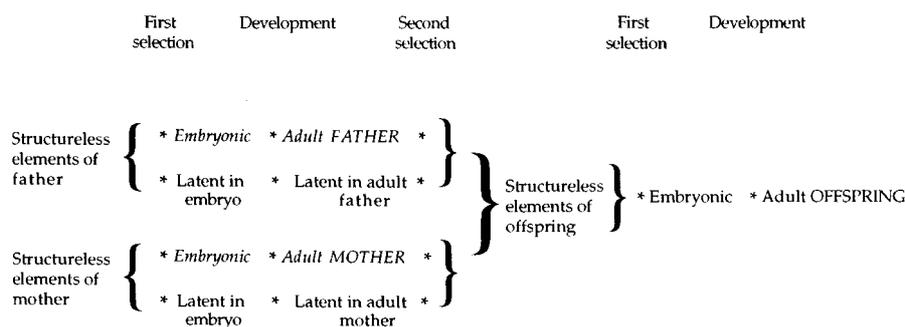


Figure 1. Relationship between parents and offspring. (After Francis Galton, “On blood relationship,” *Proc. Roy. Soc.*, 20 (1872), p. 399. The names in the top row for the processes shown by asterisks have been added.)

that had not been experimentally disproven. He published his conclusions in two papers, “On blood relationship” and “A theory of heredity,” which appeared in 1872 and 1875 respectively. In this section, I shall describe this theory, contrasting it with Darwin’s theory of pangenesis.

The theory of heredity developed in 1872 is shown diagrammatically in Figure 1. The fertilized ovum consists of a very large number of hereditary elements, each with the potential to develop into a particular cell type. Galton argues from the facts of reversion that some of these elements are expressed in the adult while others remain latent: “Each individual may properly be conceived as consisting of two parts, one of which is latent and only known by its effects on his posterity, while the other is patent, and constitutes the person manifest to our senses.”⁴¹ He supposes, as he did in *Hereditary Genius*, that the latent elements are much more numerous than the patent ones, arguing from the fact that a single strain of impure blood can reassert itself after more than eight generations, which corresponds to a dilution of 1 in 256. The primary elements in the fertilized ovum are structureless (first column in Figure 1), and a small number of them are selected (First selection) to become the patent embryonic elements which are developed (Development) into the adult person, the residue remaining latent. The patent embryonic elements are selected by a process which Galton called class representation, by which he meant that the elements in the ovum fall into a number of classes determining, if expressed, different characters, and that a small number was chosen from each class to become patent. He repeated the metaphor of the election of a “representative assembly” used in *Hereditary Genius*, but is deliberately non-committal about the method of election since nothing is known.

⁴¹ Galton, “On Blood Relationship” (above, n. 4), p. 394.

Finally, Galton considers how the patent and latent elements in one generation are transmitted via the germ cells to the structureless elements of the next. Not all the elements can be transmitted, otherwise the variety of elements would increase without bound, so that only some of them are selected (Second selection). He concludes that patent elements are transmitted more feebly than latent elements from the fact that acquired characters are rarely inherited. (The hidden assumption is that acquisition of a character would change the corresponding hereditary element.) The combination of the small number of patent elements with their small power of transmission means that the italicized lines of transmission through patent elements in Figure 1 are “a nearly sterile destination” compared with the non-italicized lines through latent elements.

In 1875 Galton restated, with some change of terminology, the theory of the mechanism of heredity put forward in 1872, and contrasted it with Darwin's theory of pangenesis. He began by coining the word “stirp” to express the sum-total of the hereditary elements, or “germs” as he now called them, which are to be found in the newly fertilized ovum. With this new terminology, his theory of heredity has four elements. (1) The stirp contains many individuals comprised of many varieties of germs. (2) Each of the enormous number of quasi-independent units (cells) in the body has developed from a separate germ in the stirp. (3) The stirp contains many more germs than there are cells in the body, so that only a small proportion of the germs develop into cells. (4) The residue of undeveloped (latent) germs contributes to the stirp of the next generation, the developed germs (with rare exceptions postulated to allow the possibility of the inheritance of acquired characters) do not and are thus nearly sterile. In 1872 Galton was non-committal about how the patent elements were selected, but in 1875 he stressed the idea of competition between germs: “We may thus compare the stirp to a nation and those among its germs that achieve development, to the foremost men of that nation who succeed in becoming its representatives.”⁴² These dominant germs which achieve development are not transmitted, with an unfortunate consequence: “Another result of the best elements of the stirp being rendered sterile, is the strong tendency to deterioration in the transmission of every exceptionally gifted race.”⁴³

Galton acknowledged his debt to Darwin's theory of pangenesis for his account of the facts to be explained, and for the idea that elements (gemmules) of different types are developed directly into the respective cell types; he also accepted Darwin's explanation of reversion that it results from elements remaining latent. But he rejected, except in rare cases, the idea that

⁴² Galton, “A Theory of Heredity” (above, n. 4), p. 336.

⁴³ *Ibid.*, p. 340.

cells throw off elements that travel freely throughout the body and aggregate in the germ cells. His rejection of this transportation hypothesis, except as a very minor process, was based on his failure to demonstrate the existence of these elements in the blood, and on his skepticism about the importance of the inheritance of acquired characters. Galton's acceptance of Darwin's idea that some gemmules develop into cells and are no longer available for transmission to the next generation, together with his rejection of the idea that cells can throw off new gemmules, led inevitably to the conclusion that only the latent gemmules are transmitted through inheritance.

The difference between the two theories is encapsulated in two quotations. Darwin concluded his summary of the theory of pangenesis: "Hence, it is not the reproductive organs or buds which generate new organisms, but the [cells] of which each individual is composed."⁴⁴ On the other hand, Galton concluded in 1872: "We cannot now fail to be impressed with the fallacy of reckoning inheritance in the usual way, from parents to offspring, using those words in their popular sense of visible personalities. The span of the true hereditary link connects, as I have already insisted upon, not the parent with the offspring, but the primary elements of the two, such as they existed in the newly impregnated ova, whence they were respectively developed."⁴⁵

Galton's rejection of the transportation hypothesis affected his theory of both sexual and asexual reproduction. In sexual reproduction, he thought, following Darwin, that the patent elements had been used to develop into somatic cells, but he did not think that developed cells throw off new elements that can accumulate in the germ cells; he was therefore led to believe that the germ cells are directly descended from the residue of latent elements that have not developed into cells. However, he allowed a very moderate transgression of this general rule to allow for the occasional possibility of the inheritance of acquired characters: "Each cell may be supposed to throw off a few germs that find their way into the circulation, and thereby to acquire a chance of occasionally finding their way to the sexual elements, and of becoming naturalised among them."⁴⁶

Galton also needed to find an explanation for asexual reproduction. Darwin thought that sexual and asexual reproduction were similar. The buds of a tree can reproduce the parent, as can a small piece of a freshwater worm. He concluded that all the different varieties of gemmule must be present in every tissue, which he explained as a result of their free travel throughout the body. Galton accepted that all varieties of gemmules must be present in all tissues, but Darwin's explanation was not open to him. He supposed that

⁴⁴ Darwin, *Variation of Plants and Animals* (above, n. 7), II, 457.

⁴⁵ Galton, "On Blood Relationship" (above, n. 4), p. 400.

⁴⁶ Galton, "A Theory of Heredity" (above, n. 4), p. 346.

the fertilized ovum contains elements (gemmules) of every variety, that the different varieties are segregated by mutual attractions into different cell lines during the first few cell divisions of the embryo, but that the segregation is inexact so that the different cell lines that will give rise to different tissues all contain a few latent elements of every variety and are thus totipotent.

In 1875 Darwin wrote to Galton, asking him how, based on his theory, he would explain the fact that if two varieties of plant (say black and white) are crossed, the hybrid is often intermediate in character (say gray); and that this hybrid could produce millions of buds all exactly reproducing the intermediate, gray character.⁴⁷ Darwin thought that this could only occur if the hybrid cells produced gray gemmules, which give rise to gray buds. Galton replied that the facts could also be explained by his hypothesis: all somatic tissue contains surplus latent gemmules from the original stirp (in this case white and black gemmules), and these surplus gemmules can give rise to gray buds, in the same way that the original gray tissue was formed.

But the most interesting part of Galton's reply was his discussion of the possible structure of the gray tissue in the hybrid. It may take only one gemmule to form a cell, or it may take several. If it takes only one, the tissue would consist of equal numbers of white and black cells, which could be distinguished under high magnification, but would look gray when less highly magnified. He continued: "If there were two gemmules only, each of which might be white or black, then in a large number of cases one quarter would be always quite white, one quarter quite black, and one half would be gray. If there were 3 [gemmules], we should have 4 grades of colour (1 quite white, 3 light gray, 3 dark gray, 1 quite black), and so on according to the successive lines of 'Pascal's triangle'. This way of looking at the matter would perhaps show (a) whether the number in each given [cell] was constant, and (b), if so, what those numbers were."⁴⁸

If Galton had applied this insight to the 1:2:1 segregation in the F₂ generation after a hybrid cross, he might have discovered Mendelism. He did in fact consider this question in 1872: "Lastly, it is often remarked (1) that the immediate offspring of different races or even varieties resemble their parents equally, but (2) that great diversities appear in the next and in succeeding generations. In which stage does the variability occur? It cannot be in the first [First selection] nor in the second (Development), else (1) could not have been true; therefore it must be in the third stage [Second selection]. A white parent necessarily contributes white elements to the structureless stage

⁴⁷ Olby, *Origins of Mendelism* (above, n. 2), pp. 55–57.

⁴⁸ Olby, *Origins of Mendelism* (above, n. 2), pp. 55–57.

of his offspring, and a black, black; but it does not in the least follow that the contributions from a true mulatto must be truly mulatto.”⁴⁹

Galton clearly has in mind in this passage that variability in the offspring of mulattos results from the process of selection of a representative sample of latent elements in the germ cells of mulatto (F₁) individuals, but he does not pursue the question further. In fact, it seems likely that Galton added this passage to the paper as an afterthought in response to a question put by Darwin to whom Galton had sent the manuscript for comment before publication.⁵⁰

Similarities Between Relatives

The weakness of Galton’s theory is that it gave him little insight into the reasons for the similarities between relatives, the question in which he was most interested. In 1872, he discussed the parent-offspring relationship in Figure 1 as follows:

We see that parents are very indirectly and only partially related to their own children, and that there are two lines of connexion between them, the one [non-italicized] of large and the other [italicized] of small relative importance. The former is a collateral kinship and very distant, the parent being descended through two stages (two asterisks) from a structureless source, and the child (so far as that parent is concerned) through five totally distinct stages from the same source; the other, but unimportant

⁴⁹ Galton, “On Blood Relationship” (above, n. 4), p. 402.

⁵⁰ Pearson quotes a letter from Galton to Darwin dated June 4, 1872, the week before Galton read the paper at the Royal Society:

Your criticisms on my paper are very gratifying to me, the more so that the question you put is one to which I can at once reply. You ask, why hybrids of the first generation are nearly uniform in character while great diversity appears in the grandchildren and succeeding generations? I answer, that the diagram shows (see next page) that only 4 stages separate the children from the parents, but 20 from their grandparents and therefore, judging from these limited data alone (ignoring for the moment all considerations of unequal variability in the different stages and of pre-potence of particular qualities etc.), the increase of the mean deviation of the several grandchildren (from the average hybrid) over that of the several children is as $\sqrt{20}:\sqrt{4}$, or more than twice as great. The omitted considerations would make the deviation (as I am prepared to argue) still greater (Pearson, *Life of Galton* [above, n. 15], II, 169).

Pearson omits the diagram because he has failed to interpret it. In the published paper, Galton replaces this view with the suggestion that variability arises at the stage of the second selection, a reconsideration that turned out to be correct.

line of connexion, is direct and connects the child with the parent through two stages.

It seems arbitrary to describe the closeness of the relationship simply by the number of stages separating parent and child without discussing the amount of variability generated at each stage. There is also a serious problem in accounting for the correlation arising from the more important, collateral line of connexion. The parent-child correlation is a correlation between patent elements. Since only latent elements are transmitted in the collateral line, this is dependent on a correlation between latent and patent elements within parents; but under the simplest model of random mating and random selection of patent elements within each class, there would be no correlation between latent and patent elements within an individual, and therefore no correlation between parent and child!

How does Galton explain the resemblance between parent and child in view of this problem? In 1872 he wrote: "I maintain that the personal manifestation is, on the average, though it need not be so in every case, a certain proof of the existence of some latent elements."⁵¹ In effect, he assumes that there is, in general, a positive correlation between the latent and the patent elements, though he has no explanation how this correlation is maintained. In fact, it requires either assortative mating (a tendency of like to mate with like) or non-random selection of the patent elements (less variability than implied by random choice). Either Galton did not appreciate this point, or he implicitly assumed a high degree of assortative mating.

In 1875, Galton suggested that some germs are dominant over others and are therefore more likely to be selected for development. He also supposed that these dominant germs would be unlikely to be transmitted to the next generation, which was predominantly recruited from the residue of undeveloped germs, and he concluded that this might give rise to a negative correlation between parent and offspring. He wrote:

The hypothesis that the developed germ is less fecund . . . than the germ that continues latent, agrees singularly well with many classes of fact. Thus it explains why, although hereditary resemblance is the general rule, the offspring is frequently deficient in the very peculiarity for which the parent was exceptionally remarkable. We can easily understand that the dominant characters in the stirp will, on the whole, be faithfully represented in the structure of the person who is developed out of it; but if the personal structure be a faithful representative of the dominant germs, it must be an over-favourable representative of the germs generally, and therefore, *a fortiori*, of the undeveloped residue; nay in extreme cases,

⁵¹ Ibid., p. 399.

the personal elements may be absolutely unrepresentative of the residual elements, the accidental richness of the sterile sample in some particularly valuable variety of germ, having drained the fertile residue of every germ of that variety. . . . Experience testifies to the fact that children of men of extraordinary genius have not unfrequently been singularly deficient in ability.⁵²

Despite this reason for expecting a negative correlation between parent and child, Galton accepted without comment that “hereditary resemblance is the general rule.”

In 1875 Galton discussed the relationship between siblings as follows:

The great dissimilarity between brothers and sisters is to be accounted for and easily illustrated by a political metaphor. We have to recognise, on the one hand, that the stirps of the brothers and sisters must have been nearly alike, because the germs are simple organisms, and all such organisms breed true to their kind, and on the other hand, that very different structures have been developed out of these stirps. A strict analogy and explanation of all this is afforded by the well-known conditions and uncertainties of political elections. We have abundant experience that when a constituency is very varied, trifling circumstances are sufficient to change the balance of parties, and therefore, although there may be little real variation in the electoral body, the change in the character of its political choice at successive elections may be abrupt.⁵³

In this passage he assumes that selection of elements for the germ cells (Second selection in Figure 1) gives rise to little or no variability, so that the stirps of brothers and sisters are almost identical. Thus differences between brothers and sisters must be due to variability in the choice of patent elements from the stirp (First choice), in other words to developmental variability.

Galton’s views on the reasons for similarities and dissimilarities between twins are very instructive. He was familiar with the existence of two types of twins: “The word ‘twins’ . . . covers two very dissimilar events – the one corresponding to the progeny of animals that have usually more than one young at a birth, each of which is derived from a separate ovum, while the other is due to the development of two germinal spots in the same ovum. In the latter case, they are enveloped in the same membrane, and all such twins are found invariably to be of the same sex.”⁵⁴ They are today called dizygotic and mono-

⁵² Galton, “A Theory of Heredity” (above, n. 4), p. 339.

⁵³ *Ibid.*, p. 336.

⁵⁴ Francis Galton, “The History of Twins, as a Criterion of the Relative Powers of Nature and Nurture,” *J. Anthropol. Inst.*, 5 (1875), p. 392.

zygotic twins respectively. In *English Men of Science*,⁵⁵ Galton suggested the use of twins to determine the relative powers of nature and nurture, and he subsequently investigated this subject more thoroughly.⁵⁶ However, his method differed from the modern “twin method” for distinguishing nature and nurture.⁵⁷

Galton took a group of thirty-five pairs of like-sexed twins who were extremely similar at birth and in childhood, and asked whether they subsequently grew unlike when they left home under the influence of different environments; in general they did not, unless one of the twins developed an illness. In contrast, he took a group of twenty pairs of like-sexed twins who were very dissimilar at birth, and asked whether their similarity of nurture in childhood and in youth tended to assimilate them; it did not. He concludes: “The impression that all this evidence leaves on the mind is one of some wonder whether nurture can do anything at all, beyond giving instruction and professional training. There is no escape from the conclusion that nature prevails over nurture when the differences of nurture do not exceed what is commonly to be found among persons of the same rank of society and in the same country.”⁵⁸

Galton’s twin method was to track the life history changes of twins to see whether twins who were similar at birth diverged in dissimilar environments or whether twins who were dissimilar at birth converged in similar environments. It is quite different from the modern twin method of comparing the similarities between monozygotic and dizygotic twins. The latter method depends on the assumption that monozygotic twins are genetically identical whereas dizygotic twins are not. Galton, on the other hand, believed that all twins, dizygotic as well as monozygotic, had identical stirps, just as siblings do, and he attributed the fact that most monozygotic twins are almost identical to the similarity of their developmental environment: “As regards the similarity of true twins, there can be little difficulty; we should expect, on statistical grounds, that the two halves of any assemblage of germs would be much alike. The secondary stirps of the twins being alike, *and the circumstances under which the bodily structure is developed out of them being almost identical*, the results must be closely similar” (my italic).⁵⁹

His remark “we should expect, on statistical grounds, that the two halves of any assemblage of germs would be much alike” suggests why he thought

⁵⁵ Francis Galton, *English Men of Science: Their Nature and Nurture* (London: Macmillan, 1874; reprinted London: Frank Cass, 1970), pp. 12–16.

⁵⁶ Galton, “The History of Twins” (above, n. 54).

⁵⁷ Richard D. Rende, Robert Plomin, and Steven G. Vandenberg, “Who Discovered the Twin Method?” *Behav. Genet.*, 20 (1990), 277–285.

⁵⁸ Galton, “The History of Twins” (above, n. 54), p. 404.

⁵⁹ Galton, “A Theory of Heredity” (above, n. 4), p. 337.

that selection of elements for the germ cells gives rise to little or no variability, since this selection amounts to taking half an assemblage of germs. The italicized clause suggests that the near identity of most monozygotic twins compared with the differences between brothers and sisters is due to the absence of developmental variability in the former.

On the other hand, Galton thought that the group of twenty twins who were markedly dissimilar were monozygotic, and he supposed that their dissimilarity was due to late division of the ovum: "We might expect that if there had happened to be a sufficient delay before the division of the primary stirp, to allow its germs to arrange themselves somewhat according to their affinities, the twin halves of the primary stirp would be strongly contrasted."⁶⁰ His reason for thinking these twins to be monozygotic was that they were all like-sexed, but he admitted that he had no direct evidence that they were monozygotic, and it seems likely that they were not.

In conclusion, Galton's ideas about the relationship between relatives at this time were confused. His theory of heredity provided no reason to explain the resemblance between parent and child, except for the unwarranted expectation of a correlation between patent and latent elements. In considering the resemblance between siblings, he supposed that they had identical genotypes (stirps) and attributed their differences to developmental variability; he discounted variability due to segregation, despite his earlier recognition of its importance in the special case of a hybrid cross.

Galton's Ideas on the Mechanism of Heredity in 1889

After 1875 Galton turned his attention to developing a statistical theory of heredity, summarized in *Natural Inheritance*. His statistical work, including his law of ancestral heredity, led him to modify his theory of the mechanism of heredity, in particular the role of latent and patent elements; but he never explicitly recognized his change of position.

In the Introduction to *Natural Inheritance*, Galton singled out three problems for special mention, of which one is the ancestral law:

A second problem regards the average share contributed to the personal features of the offspring by each ancestor severally. Though one half of every child may be said to be derived from either parent, yet he may receive a heritage from a distant progenitor that neither of his parents possessed as *personal* characteristics. Therefore the child does not on the average receive so much as one half of his *personal* qualities from each

⁶⁰ Ibid., p. 337.

parent, but something less than a half. The question I have to solve, in a reasonable and not merely in a statistical way, is, how much less?⁶¹

In this passage Galton distinguishes clearly between the phenotype (personal features) and the genotype (of which every child receives half from each parent). He believed that reversion, which gives rise to this distinction, is due to the fact that only some of the hereditary elements (the patent or personal elements) are expressed, the rest being latent or dormant, unexpressed but capable of transmission. But he has changed his viewpoint from what he believed in 1875 about the transmission of latent and patent elements. He is clearly thinking of the fraction (something less than a half) of the personal qualities that a child receives from each parent as being patent elements in the child which were patent in and transmitted by that parent. His estimate of this fraction, obtained by a rather dubious argument, was that one quarter of the personal qualities of a child were received directly from each parent, that is to say from hereditary elements patent in the parent.⁶²

This interpretation is confirmed by the discussion of latent elements in Chapter 11 of *Natural Inheritance*:

Latent elements not very numerous. – It is not possible that more than one half of the varieties and number of each of the parental elements, latent or personal, can on the average subsist in the offspring. For if every variety contributed its representative, each child would on the average contain actually or potentially twice the variety and twice the number of the elements (whatever they may be) that were possessed at the same stage of its life by either of its parents, four times that of any one of its grandparents, 1024 times as many as any one of its ancestors in the 10th degree, and so on, which is absurd. Therefore as regards any variety of the entire inheritance, whether it be dormant or personal, the chance of its dropping out must on the whole be equal to that of its being retained, and only one half of the varieties can on the average be passed on by inheritance. Now we have seen that the *personal* heritage from either Parent is one quarter, it follows that the Latent Elements must follow the same law of inheritance as the Personal ones. In other words, either Parent must contribute on the average only one quarter of the Latent elements, the remainder of them dropping out and their breed becoming absolutely extinguished.

There seems to be much confusion in current ideas about the extent to which ancestral qualities are transmitted, supposing that what occurs

⁶¹ Galton, *Natural Inheritance* (above, n. 5), p. 2.

⁶² See Bulmer, "Galton's Law of Ancestral Heredity" (above, n. 6), for a critique of the ancestral law.

occasionally must occur invariably. If a maternal grandparent be found to contribute some particular quality in one case, and a paternal grandparent in another, it seems to be argued that both contribute elements in every case. This is not a fair inference, as will be seen by the following illustration. [If 13 cards are dealt from a pack of 52 playing cards, one expects different hands to be dealt in different deals.] So I conceive it to be with hereditary transmission. No given pair can possibly transmit the whole of their ancestral qualities; on the other hand, there is probably no description of ancestor whose qualities have not been in some cases transmitted to a descendant. . . . If the Personal and Latent Elements are transmitted on the average in equal numbers, it is difficult to suppose that there can be much difference in their variety.⁶³

Galton implicitly assumes that patent and latent elements are equally likely to be transmitted, reversing his previous view that patent elements were unlikely to be transmitted since they had been developed into cells. He then argues that only half the elements of either kind can be transmitted under biparental inheritance if the total number of elements is to remain constant. Since he has estimated that a child receives one quarter of its personal (patent) elements from each parent, that is to say as elements patent in the parent, it follows that there must be equal numbers of patent and latent elements. (The hidden assumption is that an element has the same chance, one half, of becoming patent in the child whether it was patent or latent in the parent.) He then refutes the argument (which he had previously put forward) that latent elements must be more numerous than patent ones because a single strain of impure blood can reassert itself after more than eight generations, on the grounds that it ignores the stochastic nature of transmission.

Galton's theory of heredity in 1889 may be summarized as follows. Inheritance is mediated through particulate elements in the germ plasma. In bisexual inheritance each parent transmits half of his or her elements to the offspring, thus maintaining the total number of elements in successive generations. Elements may be latent or patent, only the patent ones being expressed, but a latent element may become patent in a subsequent generation. Latent and patent elements are equally numerous, they are equally likely to be transmitted, and an element has the same chance of one half of becoming patent in the child regardless of its status in the parent. Galton's views on the role of latent elements in explaining reversion had changed between 1875 and 1889. In particular he held in 1875 that latent elements were much more numerous and much more likely to be transmitted than the patent elements expressed in the phenotype; both these views were abandoned in 1889.

⁶³ Galton, *Natural Inheritance* (above, n. 5), pp. 187–189.

He explained his reason for changing his mind about the frequency of latent elements. One can understand how reflection on the statistical theory of heredity might have led him to abandon the view that patent elements were unlikely to be transmitted, since this made it much easier to explain the resemblance between parent and child. But this would also require him to abandon the view that the patent elements are transformed into cells, and are therefore not available for transmission if the transportation hypothesis is rejected. Galton does not discuss this point explicitly, but there is a hint of a new viewpoint in a passage where he likens the main line of hereditary connection between parent and child to the chain of a necklace, and their expressed personalities to pendants attached to its links.⁶⁴ This suggests that a link is not used up in making a pendant but is still available for transmission.

Discussion

Galton's theory of heredity was particulate: "Inheritance may therefore be described as largely if not wholly 'particulate' . . . I need hardly say that the idea, though not the phrase of particulate inheritance, is borrowed from Darwin's provisional theory of Pangenesis."⁶⁵ His theory was based on Darwinian gemmules, modified on account of his rejection of the transportation hypothesis.

The first modification rejects the partial blending implied by Darwin's theory, in which latent elements do not blend but patent elements do. A cross between a white and a black plant produces gray offspring in the absence of prepotency (dominance). Under Darwin's theory, the patent white and black gemmules are transformed into gray tissue, which produces gray gemmules, while the latent gemmules retain their identity; both types of gemmule find their way to the gonads and are transmitted to the next generation. Galton rejected both the idea, resulting from the transportation hypothesis, that gray tissue produces gray gemmules, which find their way to the gonads, and the proposal that the existence of gray tissue indicates the fusion of white and black gemmules. He distinguished clearly between the blending of characters in the offspring and the blending of the hereditary elements:

As regards heritages that blend in the offspring, let us take the case of human skin colour. The children of the white and the negro are of a blended tint; they are neither wholly white nor wholly black, neither are they piebald, but of a fairly uniform mulatto brown. The quadroon child of the mulatto and the white has a quarter tint; some of the children may

⁶⁴ *Ibid.*, pp. 19–20.

⁶⁵ *Ibid.*, pp. 7 and 193.

be altogether darker or lighter than the rest, but they are not piebald. Skin-colour is therefore a good example of what I call blended inheritance. It need be none the less “particulate” in its origin, but the result may be regarded as a fine mosaic too minute for its elements to be distinguished in a general view.⁶⁶

Secondly, Galton adopted Darwin’s explanation of reversion, that some gemmules develop into cells while others remain latent and capable of expression in subsequent generations, but he rejected the idea that cells produce new gemmules that could be incorporated into the germ cells. He was thus forced in the 1870s into supposing that, with rare exceptions, only the undeveloped, latent gemmules are capable of transmission to the next generation. To explain the similarity between parent and child under this model requires a correlation between the latent and patent elements within individuals, possibly due to a high degree of assortative mating. Galton probably came to realize the problem of this requirement during his subsequent statistical work on heredity. He quietly dropped the idea that patent elements are not transmitted and that they are much less frequent than latent elements in *Natural Inheritance*, though he did not discuss why he had changed his view or what was the role of patent elements in development.

Galton adopted from the start the principle of biparental inheritance, which was generally accepted in the middle of the nineteenth century, and he drew two conclusions from it. The first, which he stated in 1865, is that, if an individual inherits one half of its hereditary particles from each parent, it must inherit one quarter from each grandparent, one eighth from each great grandparent, and so on. The same point was later made by Weismann (see note 12).

The second consequence of biparental inheritance is that, if the number of hereditary particles is to remain constant from one generation to the next, an individual can only transmit half of its particles to each offspring. In 1872 Galton wrote: “As regards the large variety of adult elements, they cannot all be transmitted, for the following very obvious reason – the corresponding qualities of no two parents can be considered exactly alike; therefore the accumulation of subvarieties, if they were all preserved as the generations rolled onwards, would exceed in multitude the wildest flights of rational theory. . . . The contributions from the latent adult elements are therefore no more than *Representative*.”⁶⁷

In 1875 he formulated the concept more precisely in terms of the number rather than the varieties of elements in a very interesting passage in which

⁶⁶ Ibid., p. 12.

⁶⁷ Galton, “On Blood Relationship” (above, n. 4), p. 397.

he proposed two arguments for the advantage of biparental (sexual) over uniparental (asexual) reproduction. The first is similar to the modern argument of Muller's ratchet.⁶⁸ His second argument is this: "There is yet another advantage in double parentage, namely, that as the stirp whence the child sprang, can be only half the size of the combined stirps of his two parents, it follows that one half of his possible heritage must have been suppressed. This implies a sharp struggle for place among the competing germs, and the success, as we may infer, of the fitter half of their numerous varieties."⁶⁹ This passage is unconvincing today as an argument for the advantage of biparental reproduction, but it clearly states the necessity of halving the number of hereditary elements.

Weismann similarly concluded in 1887 that there must be a "reducing division" during gametogenesis in which the number of hereditary elements in the nucleus is halved and he suggested that this reducing division would inevitably give rise to variability in the germ-cells: "It is quite impossible for the 'reducing division' of the nucleus to take place in an identical manner in all the germ-cells of a single ovary, so that the same ancestral germ-cells would always be removed in the polar bodies. But if one group of ancestral germ-plasms is expelled from one egg, and a different group from another egg, it follows that no two eggs can be exactly alike as regards their contained hereditary tendencies; they must all differ."⁷⁰ He attributed differences between siblings including dizygotic twins, to this fact, and also used it to account for the similarity of monozygotic twins.⁷¹ Galton had recognized the need for halving the number of hereditary elements in biparental inheritance, but he did not connect it with the origin of genetic variability. He knew that the grandchildren of a black and white couple have a variety of skin colors, and he recognized in 1872 that this must be generated by differences in the germ

⁶⁸ H. J. Muller, "The Relation of Recombination to Mutational Advance," *Mutat. Res.*, 1 (1964), 2–9. Muller wrote: "An asexual population incorporates a kind of ratchet mechanism, such that it can never get to contain, in any of its lines, a load of mutations smaller than that already existing in its at present least-loaded lines. However, the latter lines can . . . become more heavily loaded by mutation." Galton argued that, in uniparental reproduction, "At each successive stage there is always a chance of some one or more of the various species of germs in the stirp dying out, or being omitted . . . From time to time this chance must fall unfavourably . . . If the loss be vital, this particular line of descent will of course be extinguished at once; but on the more favourable supposition, the race will linger on, submitting to successive decrements in its constituent elements, until the accumulation of small losses becomes fatal . . . On the other hand, when there are two parents, . . . the chance deficiency in the contribution from either of them, of any particular species of germ, tends to be supplied by the other."⁶⁹

⁶⁹ Galton, "A Theory of Heredity" (above, n. 4), pp. 333–334.

⁷⁰ August Weismann, "On the Number of Polar Bodies and their Significance in Heredity," 1887, in Poulton, Schönland and Shipley, *Essays upon Heredity* (above, n. 14), p. 379.

⁷¹ *Ibid.*, pp. 379–381.

cells of the mulatto (F_1) individuals (see quotations above referenced as notes 48 and 66), but he never generalized this intuition.

It has been argued that Galton foreshadowed Weismann's theory of the continuity of the germ-plasm, but this is only true in a weak sense. Weismann assumed "the existence in the germ-cell of a reproductive substance, the *germ-plasm*, which cannot be formed spontaneously, but is always passed on from the germ-cell in which an organism originates in direct *continuity* to the germ-cells of the succeeding generations. . . . The germ-cells alone transmit the reproductive substance or germ-plasm in uninterrupted succession from one generation to the next, while the body (soma) which bears and nourishes the germ-cells, is, in a certain sense, only an outgrowth from one of them."⁷² One consequence of this theory of "hard" heredity is that it makes impossible the inheritance of characters acquired by somatic cells, since they are a dead end, making no contribution to the next generation.

Galton concluded his discussion of the inheritance of acquired characters in 1865 with the sentence: "We shall therefore take an approximately correct view of the origin of our life, if we consider our own embryos to have sprung immediately from those embryos whence our parents were developed, and those from the embryos of *their* parents, and so on for ever."⁷³ Karl Pearson regarded this statement as amounting to Weismann's theory of the continuity of the germ plasm,⁷⁴ but there is an important distinction. Galton expresses an idea similar to Weismann's in less precise language (using the term "embryos" instead of "germ-plasm"). He also employs the qualifying word "approximately" and, in effect, reverse the argument. For Weismann, the continuity of the germ-plasm is an empirical fact which makes the inheritance of somatically acquired characters impossible; for Galton, the empirical fact is that the inheritance of acquired characters is of little, if any importance, so that inheritance can be regarded as taking place from embryo to embryo.

With regard to Galton's theory of the 1870s, Romanes wrote that "there is not merely resemblance, but virtual identity, between the theories of stirp and germ-plasm . . . Galton anticipated by some ten years all the main features of Weismann's theory of heredity."⁷⁵ However, Weismann thought that there was a fundamental difference between the two theories: "According to my idea, the active and the reserve germ-plasm contain precisely similar primary constitutes, gemmules, or determinants; and on this the resemblance of a child

⁷² August Weismann, *The Germ-Plasm: A Theory of Heredity*, trans. W. Newton Parker and Harriet Ronnfeldt (London: Walter Scott, 1893), p. 9.

⁷³ Galton, "Hereditary Talent and Character" (above, n. 3), p. 322.

⁷⁴ Pearson, *Life of Galton* (above, n. 15), II, 81.

⁷⁵ George John Romanes, *An Examination of Weismannism* (London: Longmans, Green and Co, 1893), p. 59.

to its parent depends. The theory of the continuity of the germ-plasm, as I understand it, is not based on the fact that each 'gemmule' necessary for the construction of the soma is present many times over, so that a residue remains from which the germ-cells of the next generation may be formed: it is founded on the view of a special adaptation, which is inevitable in the case of multicellular organisms, and which consists in the germ-plasm of the fertilised egg-cell becoming doubled primarily, one of the resulting portions being reserved for the formation of germ-cells."⁷⁶

Thus there is some resemblance between the views of Galton and Weismann due to the fact that they believed that the inheritance of acquired characters is rare (Galton) or impossible (Weismann). But Galton did not forestall the essential part of Weismann's theory, the partially-mistaken idea that the germ-plasm of the zygote is doubled, with one part being reserved for the formation of the germ-cells.⁷⁷

Galton failed in his attempt to construct a workable, physiological theory of heredity, but his failure is of interest today for several reasons. His failure to recognize the role of segregation in generating genetic variability led to his failure to understand the real distinction between monozygotic and dizygotic twins; this is why he did not develop the modern "twin method" for estimating heritability. His emphasis on the role of latent and patent elements in heredity, which he adapted from Darwin's theory of pangenesis, underpinned his most important contributions to biology: parent-offspring regression and the law of ancestral heredity.⁷⁸ Most important of all, his failure to construct a physiological theory of heredity underlines the difficulty faced by supporters of Darwinism in the nineteenth century in understanding how natural selection worked.⁷⁹

⁷⁶ Weismann, *The Germ-Plasm* (above, n. 72), p. 200.

⁷⁷ The irreversibility of translation from DNA into protein is today thought to be the real obstacle to the inheritance of acquired characters, rather than the separation of germ cells from somatic cells, which does not hold in plants or lower animals; see Leo W. Buss, *The Evolution of Individuality* (Princeton University Press, 1987).

⁷⁸ See Bulmer, "Galton's Law of Ancestral Heredity" (above, n. 6).

⁷⁹ See Gayon, *Darwinism's Struggle for Survival* (above, n. 1).