My dear Fisher,

In answer to your letter concerning my father's views on the laws of inheritance, it seems to me that we should first of all look to his theory of pangenesis; for that was his theoretical way of accounting for what he believed to be the facts. We may be disinclined to tread this path once more; for we know in advance that we shall again reject this theory as a whole. Nevertheless it is the best way, I think, of ascertaining what were his underlying thoughts. If I quote numbers, they will be the pages in *Animals and Plants under Domestication II* second edition.

According to his theory, each cell gives off gemmules, and "several gemmules are requisite for the development of each (new) cell or unit" (381), presumably some of them coming from each parent. Though not, I think clearly stated, I gather that he held that these necessary gemmules blended completely, so that the parts, when fully developed on such a basis, in their turn, gave off gemmules "which ultimately developed into units like those" (370) formed by this process of blending.
This blending of the gemmules, though complete, was not uniform; for at all events the gemmules "derived from one parent may have some advantage in number, affinity or vigour over those derived from the other" (382). These gemmules are also held to be "capable of transmission in a dormant state to future generations and may then be developed" (370). For both these reasons, organisms will only be "generally nearly intermediate in character between their two parents" (395).

Now the more unequal the blending of the formative gemmules, the greater the "host of long-lost characters (which) lie ready to be evolved under proper conditions" (369), the more "incessantly" (394) reversion acts, the longer would it take for complete uniformity to be created in any interbreeding group. "After a longer or shorter period, the species will tend to become nearly uniform in character from the incessant crossing of individuals" (362); but the time might be fairly long. And all this time selection would go on whether or not any other changes were taking place. Moreover "the dissimilarity of" sibs and the greater variety of sexually-produced organisms would be accounted for by the "unequal blending of the characters of the two parents" and by the "reversion to ancestral characters" (239); but all this nevertheless points to a slow but complete process of blending.
In order to account for progressive evolution, he held that the surroundings of an organism affected its development and that normally the gemmules subsequently thrown off represented the form as that produced. The transmission of latent gemmules for many generations merely threw back the environmental cause into the past. With "absolutely uniform conditions of life, there would be no variability" (242) nor any progress.

In passing may not all mutations be due to some environmental cause? The regularity with which they appear in Drosophila no doubt tempts us to look on it as an inevitable natural process. But the more uniform the surrounding, the more regularly will exceptions appear as a rule. If the mutations in that fly are due to thunderstorms, they would come in one year about as much as in another. And our knowledge of the effects of X rays on organisms and lightning on our wireless sets makes this illustrative supposition less ridiculous.

My belief is that my father had no clear distinction in his mind such as we have between mutations and mendelian differences. All variations were much the same to him though I think he says somewhere, I cannot say where, that some are not inherited. Otherwise in identical surroundings variations identical in form differ in hereditary effects solely because of differences in the latent gemmules which they carry. The amount of variation depends solely on the amount of exceptional environmental
effects; this being, he held, proved by the effects of domestication. I think there is more truth in this last contention than you apparently do. But his system allowed for nothing like the accumulated effects of mutations.

In pangensis an effort was being made by my father in the direction indicated by his letter of 1857, so it seems to me. Fertilization, he then said, is "a sort of mixture and not true fusion"; and, according to pangensis, the ancestral gemmules whilst latent do not fuse. This was a step in the direction of mendelism. He held that "each element of the body" had an "independent life" (365), and if he had not come under the influence of a few Lamarckians whom he admired so much, he might have hit on a different idea of pangensis. He might have seen that each cell contained a basis more or less capable of causing the development of the whole organism. He did realize that hybrids, when united, led to reversions to either parental type (398), his explanation being much the same as ours. "Reversion depends on the transmission from the forefather to his descendants of dormant gemmules" (399). Replace "dormant gemmules" by "recessive genes" and we have pure mendelism. He felt bound, and he was bound from his point of view, to make his theory cover the inheritance of acquired characters and telegony. Pangensis is, I hold, a logical system, and being "provisional" it should only serve to indicate
his general beliefs. It is hardly more difficult to believe than mendelism, when we realize what marvellous powers we attribute to the genes of a single cell, enabling them to control the whole growth of an organism through all its many phases. But pangenesis fails to account for the numerical effects discovered in connection with mendelism, for correlation coefficients, and for the accumulated affects of variation, and it must, therefore, be rejected.

Some Lamarckians, who go further than my father in such beliefs, have sneered at pangenesis, without themselves attempting to frame a rival theory. For this I should like to give them one in the eye.

All this, however, if accepted does not seem to me to necessarily alter your views materially. The blending which my father believed in was, I think, less rapid than you seem to suppose; and I do believe that the great variability of domestic animals is partly due to mutations having been exceptionally frequent under domestication.

Possibly we should take a leaf out of my father’s book and be sure that our theory accounts for all that we hold to be true. A graft of a plum, which seeds truly, if placed on another stock, loses this power and becomes variable (247). Sometimes "more than one spermatozoon
is requisite to fertilize an ovum" (356). Tubers of a potato "produced from a bud of one kind inserted into another are intermediate in their qualities". (360). We may yet have something to learn.

Yours sincerely,

Demond Danori

P.S. I am inclined to think that "definite variations" are best translated by "acquired characters" and "indefinite variations" by "mutations"—only on one then suspected the possibles of the segregation of "genes" involved.