Heredity, Environment, and Politics[1]

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LESS THAN TWENTY-FIVE YEARS AGO, there was thought to be no way by which environmental conditions could bring about hereditary changes in organisms. Since that time, more and more environmental agents capable of inducing hereditary changes have been discovered: first, temperature and x-rays; then, other ionizing radiations and ultraviolet light; more recently, chemicals such as colchicine, mustard gas, and formalin. These agents alter the chromosomes in both body cells and germ cells, but only the effects produced on the germ cells, or cells from which they are derived, are inherited in sexual reproduction.

About forty years ago, the only well-established types of inheritance were Mendelian and sex-linked, both of which proved to have their bases in the chromosomes. Since that time, there has gradually accumulated a number of examples of non-Mendelian inheritance: first, plastid inheritance; then, plasmon inheritance and Dauermodifikationen; more recently, a type of inheritance determined by cytoplasmic particles known as plasmagenes, with properties like those of nuclear genes and viruses.

Modern genetics has thus gone a long way from its earlier state of knowledge, but it still is a vigorous, young science and is growing rapidly. The question we consider here is whether it is now undergoing a profound metamorphosis into a form with no more readily recognizable relation to its earlier stage of existence than a moth has to a caterpillar. The Chromosome Theory of Heredity and the Theory of the Gene have been declared no longer valid. The growing list of environmental agents that can alter heredity has been declared but a small and relatively insignificant fraction of the genetically active environmental agents. The central feature of the new genetics is held to be the demonstration that acquired characters are not only inherited, but that this is the usual thing.

Establishment of these principles would indeed constitute a profound metamorphosis of genetics; but most professional geneticists refuse to admit their validity. The inheritance of acquired characters is viewed by many of them as an outmoded superstition. Whether right or wrong, this attitude is at least understandable in view of the record. Of the many previous attempts to demonstrate experimentally the inheritance of acquired characters, all have failed. In most cases, the attempts yielded negative results. When positive results were claimed, the work later proved to be fraudulent, indecisive, or incompetently performed; repetition with unobjectionable methods always failed to establish the claims. No wonder most geneticists consider the matter closed.

It takes unusual circumstances to arouse lively interest among geneticists concerning a theory that seems so fully discredited. Unusual circumstances indeed are associated with the newest champion of the inheritance of acquired characters, Trofim Denisovich Lysenko, who has come increasingly into public attention since 1932. These circumstances make the currently debated issues of great importance to every biologist and indeed to every citizen of the world. Lysenko's views have been accepted both by a great nation noted for its interest in and support of science, and by a highly organized, vocal, active, but nonscientific group, distributed throughout the world; moreover, this nation and this group consider the matter of sufficient importance to root out and remove the opposition. This fact places the subject of the inheritance of acquired characters in an entirely new position; it cannot, in this case, be considered as merely a biological controversy. But we must not confuse the issues. For purposes of analysis and understanding, the biological and the political aspects of the matter must be separately and objectively considered. This I shall attempt to do.

Some explanation of my intention to consider the biological aspect of Lysenkoism is perhaps due those of my colleagues who, after careful consideration, maintain that the controversy is not a scientific one at all. That there is a strong political and philosophical element in the controversy cannot be denied, as I shall later show. Nevertheless, I believe many biologists and others hold that the political support given to a biological theory and its agreement with a particular philosophy may be irrelevant with respect to its scientific validity. They have, it seems to me, the right to demand objective, critical consideration of the claims of the new genetics, so that they themselves can decide the extent to which the controversy is or is not scientific. Although both are important, the judgments we reach on the biological claims should be entirely independent of our judgments on the nonscientific aspects of the controversy.

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As the latter have been dealt with extensively by others and are doubtless familiar to all of you, I shall merely touch upon them briefly towards the end of this paper, and shall devote nearly all of my time to a discussion of the biological questions that have been raised.

In reporting and evaluating the work of the Lysenkoists, the language barrier is a source of difficulty. Fortunately, there are three excellent sources of information in English. First is Lysenko's (*9*) treatise of 1943 *Heredity and Its Variability,* translated into English by Dobzhansky. Second, the booklet *The New Genetics in the Soviet Union* by Hudson and Richens (*6*), published in 1946, gives a critical review of about 200 Lysenkoist publications. Third, *The Situation in Biological Science* (*21*), a book published in 1949, contains 58 Russian papers translated into English. Two of these papers are by Lysenko and are his latest statements available in English. They form the basis of my account of his current views.

Lysenkoism: Observations and Interpretations

To be clear and critical, an account of the work and views of the Lysenkoists must make a clean separation between observations and interpretations. Lysenko's statement of his case for the inheritance of acquired characters involves three main classes of observations, each centering about a different method. However, the papers of Lysenkoists also contain other observations of interest in relation to physiological problems. These observations should not be ignored or rejected, even if one should object to the work of the Lysenkoists on the inheritance of acquired characters. They will not be discussed here, however, because in my opinion they do not bear on the genetic question under discussion. The following account will be limited to the observations reported when the three principal methods just mentioned were employed.

The first method is simply to cross different breeds; to rear the hybrids and later generations under conditions best adapted to the type of organism one wishes to obtain; and in each generation, to select for further breeding those individuals that thrive best under these conditions and that most closely manifest the desired characteristics. An important part of the method is to select for the crosses breeds that, by their traits and their range of variation, show promise of yielding after hybridization organisms of the type desired. Using this method of sexual crossbreeding and selection, the Lysenkoists claim to have obtained new breeds of organisms of the sort they set out to obtain.

The second method consists of grafting together two different breeds of plants, especially when the two plants differ in age, one being young and the other mature. According to the Lysenkoists, seeds obtained from *one* component of the graft combination (especially the young component) yield plants with mixed characteristics, some resembling characteristics of one component of the graft combination and some resembling those of the other component in the graft combination. Again, these seeds (and later generations) are grown under specially suitable conditions and deliberate selection is exercised in the choice of plants to yield seed for later generations. This grafting method is reported to have yielded results with a number of plants, especially with tomatoes.

Both of these methods were earlier used by Michurin. They play so important a part in Lysenkoism that this work is usually referred to as Michurinism.

The third method is to expose plants to altered environmental conditions at a certain stage of life and to repeat this for two to four successive generations, selecting for treatment in each generation plants derived from parents most nearly conforming to the type one wishes to obtain. With this method, it is claimed that the desired types were obtained and that they reproduced true to type without further treatment in later generations. The chief observations have been made on cereals, especially wheat and rye, but other plants have also been employed.

We may now turn to the interpretations as a separate and distinct matter. Lysenkoists maintain that the results obtained with all three of the methods are due to the inheritance of acquired characters. When the traits of a plant are modified by subjection to a particular environmental treatment and, after several generations of treatment plants show the new traits without requiring the environmental treatment, it is concluded that the effects of the treatment have become hereditary. When the right environmental conditions are applied at the correct stage of the plant's life, its normal heredity is held to be destabilized and rendered readily alterable by environment.

With respect to the results of grafting, it is held that the two components of the graft form a single unitary organism in which the parts united by grafting interact to destabilize the heredity of each under the influence of the heredity of the other. This assumed interaction is believed to form a hybrid, a graft or vegetative hybrid, entirely comparable to the hybrids formed by the union of gametes in sexual reproduction. The formation of seeds on one part of the graft combination, which develop into plants showing some characteristics of the other part of the graft combination, is interpreted as inheritance of characteristics acquired from a graft partner. There is another essential feature of the interpretation: the assumed mixed inheritance of the seeds is held to be unstable and environmental conditions are again presumed to determine which hereditary traits become stabilized.

The results obtained by the ordinary method of sexual crossbreeding and selection are interpreted in a similar way. The union of two sexual cells from two different breeds brings together two diverse heredities. This, as in the case of the assumed graft hybrids, is believed to destabilize heredity so that the environmental conditions can bring about and stabilize new hereditary constitutions.

Because they believe these experiments demonstrate the inheritance of acquired characters, the Lysenkoists conclude that heredity cannot be based on any isolated special substance. All parts of the plant and all parts of each cell—even the sap—are believed to be materials of heredity which form an intimately interacting genetic system. As this conclusion is inconsistent both with the isolation of the germ plasm and with the chromosomes as the sole material basis of heredity, they conclude further that these views are false. Believing them to be essential features of neo-Mendelism, they discard the whole of neo-Mendelian genetics.

A Revolution in Genetics?

The interpretations of the Lysenkoists, taken as a whole, are thus in fundamental disagreement with what has been regarded as valid generalization from countless observations. To judge the scientific legitimacy of so complete a revolution, we must seek answers to three questions: (1) Are the experiments decisive for the proposed interpretations? (2) Do these interpretations account for observations that cannot be accounted for by the previous well-tested generalizations? (3) Do these interpretations provide a simpler or more reasonable explanation for all or most of the available observations?

Neo-Mendelism

It may be said at once that the Lysenkoist interpretations do not and cannot account for the facts of neo-Mendelism, particularly the quantitative facts. The Mendelian ratios in inheritance, confirmed countless times for a great variety of hereditary traits in microorganisms, plants, animals and man, by investigators in all countries of the world in which biological science is cultivated, including Russia—and even by beginning students in biology—find no place in the new genetics. Lysenkoists do not admit the cogency of the numerical facts of observation that form the starting point and basis of Mendelian genetics. Their opposition is based on four points.

First, they claim that the Mendelian ratios are due, not to the segregation and recombination of genes, but to the action of environment upon hybrids whose heredity is destabilized by the very fact of being hybrid. In support of this claim, they report that the ratios vary with the environmental conditions. In this connection, two facts should be noticed. Disturbances of Mendelian ratios due to differences in viability of the segregating classes are well known to geneticists, and environmental conditions are known to affect the proportion that survives; but the influence of environment on *survival* of a class does not justify concluding that environment determines the *production* of that class. More important, the interpretation that environment determines the production of the segregating classes completely fails to account for the common observation of definite segregation ratios such as 3:1.

Second, the Lysenkoists maintain that some hereditary traits fail to show the 3:1 ratio. Examples from Michurin's work on fruit trees and from the work of others are cited as evidence. This fact is not disputed by Mendelian geneticists. Indeed they can provide many more examples, as the textbooks of genetics show. The difference appears in the way this fact is handled. The Lysenkoists seem to argue that if one can find cases in which the 3:1 ratio does *not* occur, then the innumerable cases in which it *does* occur can be of no significance. The Mendelians on the other hand have used these other ratios as critical tests of their chromosome and gene theories. They reasoned that if these theories are correct, each ratio should be correlated with predictable and observable features of chromosome behavior. Their amazing success in demonstrating such correlations in the study of sex-linked inheritance, nondisjunction, linkage and crossing over, polyploidy, heteroploidy, inversions, translocations, deficiencies, and duplications leaves no possibility of legitimate doubt as to the direct relation between the ratios observed in breeding experiments and the behavior of the chromosomes observed through the microscope.

The third objection made by the Lysenkoists is their claim that attempts to repeat the basic experiments, such as Mendel's pea crosses, did not yield the 3:1 ratio. The data purporting to show this (according to Hudson and Richens, *6*) were analyzed by Kolmogorov and shown not to differ significantly from the 3:1 ratio; he considered the data to be, on the contrary, a confirmation of Mendel.

This brings us to the fourth objection, which is a most important one. Lysenko holds that statistics should have no place in biology because it represents incertitude. By rejecting statistics, Lysenko rejects statistical analysis of the significance of results, including the repetition of Mendel's crosses, and at the same time rejects all statistical aspects of genetics. Let us be entirely clear on this. The Lysenkoists are not maintaining that statistics has been badly applied; they claim it is *inapplicable* to biology and that *any attempt* to apply it is *unscientific.* As scientists, you will not wish or need me to justify the use of statistics in biology or to draw the obvious conclusions.

It is important, however, to realize that Lysenko's rejection of neo-Mendelism is not merely rejection of an interpretation. He denies some of the basic facts of observation (e.g., the 3:1 ratio); he ignores other basic facts of observation (the large number of correlations between chromosome behavior and the ratios obtained in breeding experiments); and he rejects as unscientific the methods of statistics used by biologists the world over.

It must therefore be concluded that justification of the revolution in genetics proposed by the Lysenkoists cannot be based on its providing a more reasonable explanation than the current one for the previously available observations. It provides no explanation whatever for the quantitative results or for the observed relation between chromosome behavior and breeding results. This alone is sufficient ground for concluding that the Lysenkoists have no new genetics that can take the place of the genetics current elsewhere.

The Inheritance of Acquired Characters

Yet, the contribution of the Lysenkoists could still be a considerable one, even if less than they claim, provided they presented decisive evidence for phenomena previously undemonstrated, particularly if these phenomena could not be accounted for by the previous corpus of genetic generalizations. For example, if their observations on environmental action, on grafts, and on sexual hybrids justified their interpretation of the inheritance of acquired characters, this would indeed be a great contribution. We must therefore examine the evidences in relation to that interpretation.

Let us consider first the most direct evidence, the evidence that purports to have demonstrated the inheritance of acquired characters by exposing plants to the action of effective environmental conditions during a sensitive phase of their life history. The claims as to inherited effects of vernalization may be taken as the typical and main example.

Winter wheat ordinarily must spend the winter in the field, not maturing until the following fall; but if the seeds are moistened and the seeds or seedlings are exposed for a period to low temperature, seeds planted in the spring will yield mature plants in the same year. This treatment is known as vernalization. Some breeds of wheat—spring wheats—mature in the same year without vernalization. Lysenko claims that, after a few generations in which the vernalization treatment was applied to winter wheat, he ended up with wheats that did not require the vernalization treatment. He maintains this evidence demonstrates that the effects of the vernalization treatment have become inherited, winter wheat being transformed into spring wheat.

According to Lysenko, success depends upon exploiting what he calls "phasic development." He holds that organisms develop in a sequence of phases or stages, each of which requires certain conditions. The mode of development in later stages depends on how development proceeds at each earlier stage. By subjecting the organism at a certain stage to unusual conditions, this stage will develop in an unusual way and, consequently, later stages will also be modified. Up to this point in his argument, there is little ground for disagreement. When he goes beyond this, however, and claims that the induced alteration in development is inherited by later generations, his claims are in direct opposition to the experience of others.

A close parallel to Lysenko's method is to be found in work of a sort initiated long ago by Richard Goldschmidt on animals. He also found that the development of an organism could be altered by applying appropriate environmental conditions to a definite stage of development. Moreover, the effects produced were apparently copies of the effects of known gene mutations. He therefore called these effects "phenocopies." But Goldschmidt and his followers report that phenocopies are limited to the individuals directly exposed to the unusual environment; the next generation develops as if it had never been exposed to those conditions. Thus, the method employed by Lysenkoists does not give similar results in the hands of other workers. What is the explanation of the discrepancy?

The answer to this question is suggested by the published accounts of the experiments performed by the Lysenkoists. As Hudson and Richens pointed out, serious possible sources of error in the experiments were not controlled. First, the Lysenkoists made no claim to have used sterile soils. Hence, *one seed* of spring wheat in a plot sown with winter wheat could yield some of the results reported. In Lysenko's first claim of success, *a single seed* from the entire plot came through the initial treatment and gave rise to all the later generations of spring wheat! In some of the later work, however, success has been reported for high proportions of the treated plants.

Secondly, the accounts of the experiments make no mention of controls, of parallel plots planted with untreated seeds. It is therefore not clear that the initial batch of seeds was uniformly of one kind; the possibility remains that the seeds sown included some seeds of spring wheat. Third, in the absence of adequate controls, it is not clear that the seeds were genetically pure. If they had from the start been hybrid for the traits which were to be selected, the subsequent selection of the desired types would conform strictly to previous knowledge of Mendelian segregation. Still other possibilities of error have been pointed out; but those that have been mentioned are enough to make clear that nothing whatever can be legitimately concluded from the published accounts except that the experimenters should repeat the experiments with adequate controls.

Let us now turn to the work with the grafting method. In apparent support of the claims of the Lysenkoists are examples in which an effect is known to be transmitted from one to the other part of a graft combination. Is then the difference between the claims of the Lysenkoists and others the relatively trivial one of whether a phenomenon is rare or common?

No, the difference is a fundamental one. Certain traits—so far as now known, nearly all—are held by the Mendelians to be determined by chromosomal genes. These genes and chromosomes do not wander about from cell to cell. Hence, according to the Mendelians, a graft pure for one such trait (e.g., yellow fruit) and a stock pure for an alternative trait (e.g., red fruit) could not produce a seed that is hybrid for these traits except by union of a pollen nucleus of one kind with an egg cell of the other kind. However, the Mendelians agree that certain genetic particles—call them viruses or plasmagenes as you wish—can migrate between stock and graft, but very few traits are known to be determined by such migratory particles.

On the other hand, the Lysenkoists—denying the validity of the gene theory—maintain that the sap carries the physical basis of the *entire* heredity of the plant. As the sap is free to move between stock and graft, they claim that the material basis of the *full* heredity of each may readily be carried into the other.

Thus both the Mendelians and the Lysenkoists agree that the material basis of certain exceptional traits could pass between stock and graft, but they differ fundamentally with respect to this possibility for the usual kind of trait. The critical test therefore is to follow traits of the common sort, which the Mendelians claim to be determined by chromosomal genes. With reference to such decisive traits, the experience of the Lysenkoists is in fundamental opposition to the experience of Mendelians.

The experience of the Lysenkoists may be summarized by two quotations from Lysenko himself. "*Any* character may be transmitted from one breed to another by means of grafting *just as well* as by the sexual method" (*21*, p. 39). Further, "*every* graft of a phasically young plant produces changes in heredity" (*21*, p. 608). Among the Mendelians, perhaps no one has had more experience in this field than M. B. Crane, of the John Innes Horticultural Institute. He summarized his experience recently as follows (*2*):

> I have been profoundly interested in the growing, breeding and grafting of plants and trees for nearly fifty years, and have raised thousands of fruit trees from seed; grown many both on their own roots and (as grafts) on the roots of others. I have also grafted twigs of an old variety on a young seedling on its own roots and also twigs of young seedlings onto old varieties. . . . In all these [which he enumerated in detail] there has not been the slightest indication of the different roots [i.e., stocks] having had *any* influence on the seedlings [i.e., grafts]. That is to say in my experience no vegetative hybridization occurred.

Thus, what is reported by Lysenkoists as the common and usual result is not found at all in the experience of Crane in the course of nearly fifty years of intensive investigation. And Crane's results are typical of those of the Mendelians, although some contradictory observations have been recorded. Again, therefore, we are faced with differences in the facts of observation that cannot be lightly put aside. To what is the discrepancy due? Hudson and Richens give a careful analysis of the work prior to 1946. They point out in it a number of serious experimental deficiencies, of which I will cite only two. First, in much of the work controls were not reported. Obviously, it is essential that the plants used in grafting be tested to demonstrate that they were not already, before the grafts were made, hybrid for the characters under investigation. According to the reports of those who have seen Lysenko's plants and his experimental plots, the plants employed were genetically highly mixed, so that this could be a serious source of error. Second, in much of the work no mention is made of bagging the flowers to prevent fertilization by pollen from the other part of the graft combination and from other plants. It is absolutely essential that this possibility also be controlled, for it involves another mechanism known to be capable of yielding the observed results. Until these and other sources of error are shown by adequate evidence to have been avoided, the Lysenkoist interpretation remains unjustified.

There is a more general criticism raised by Hudson and Richens against the validity of the interpretations of work by both of the methods we have discussed. You will recall that the Lysenkoists claim to obtain success with both of these methods only when the proper environmental conditions are employed. Their own failures and the failures of others to confirm their results are attributed to failure to use the proper conditions. Yet the proper conditions remain unspecified and, presumably, unspecifiable. So long as all failures are attributed to unknown causes, the hypothesis becomes elastic, essentially incapable of critical testing, and therefore useless.

We are now left with only the results of their first method, the ordinary sexual hybridization of different breeds followed by selection for a desired type under favorable environmental conditions. Lysenko maintains that heredity is so destablilized by mixing two heredities that environment can then readily impress upon the progeny of the hybrids the desired traits. For the interpretation that the traits selected are due to the action of the environment *not one bit of evidence is presented.* Moreover, it will be apparent to everyone with the least acquaintance with genetics that the *observations* reported are precisely what happens according to neo-Mendelism. Among the progeny of a hybrid, the factors or genes recombine in all possible ways and provide a variable group of individuals from which one can readily select diverse types. If the organisms that are hybridized are themselves genetically impure, or hybrid, still greater variability arises and selection can accomplish even more. The Lysenkoist interpretation of the results obtained with this method is thus entirely gratuitous. The results are expected on classical theory and no evidence or cogent reason is given to justify substituting a different explanation.

The materials on which to base answers to the three questions raised earlier are now before us. (1) The experiments of the Lysenkoists are *not* decisive for their interpretations. The experiments performed with two of their three methods lack the necessary controls and precautions; and the third method gives results in complete agreement with neo-Mendelism, without providing any evidence warranting a different interpretation. (2) No observations have been reported by the Lysenkoists which, when stripped of interpretation, cannot be accounted for by the previous well-tested principles of neo-Mendelism. (3) The Lysenkoists' interpretations do not provide a simpler or more reasonable explanation for the facts of genetics; on the contrary, they provide no explanation whatever for most of these facts.

Implications of Recent Work on Paramecium

However, regardless of whether the work of the Lysenkoists justifies their interpretation, recent work of others—particularly on the genetics of microorganisms—has been held in certain quarters to lead to the same conclusions, namely, that neo-Mendelism is invalid and that acquired characters are inherited. In the time at my disposal, I cannot discuss all the works that have been cited in this connection, so I choose from among them two recent investigations by my associates and myself on the unicellular animal *Paramecium* (*15*), for these are representative and illustrate well the main points.

The first investigation concerns the killer trait. Killer strains of paramecia liberate into their culture medium a substance that, under ordinary circumstances, kills paramecia of other strains, known as "sensitives." The killer and sensitive traits are hereditary through vegetative reproduction, self-fertilization, and conjugation between two that are alike in these traits; but when two that are unlike are crossbred, these traits follow the cytoplasm in inheritance.

The killer trait has been shown to depend upon the presence of visible, cytoplasmic particles, called kappa, of which there are a number ranging from hundreds to a thousand or more in the cytoplasm of each cell in a killer strain, but none at all in the cytoplasm of the cells of a sensitive strain (*10, 11*). These kappa particles multiply and never arise *de novo*; they can mutate and then reproduce true to the mutant form (*3, 4*). Here, then, is a particle that determines a hereditary trait of the paramecia, but is not a nuclear Mendelian gene.

Moreover, environmental conditions can alter this trait through their action on kappa (*5, 10, 13*). X-rays, nitrogen mustard, temperature and, even the amount of available food can bring about decreases in the amount of kappa (*10*) until in some paramecia none is left at all. This is an irreversible transformation of hereditary killers into hereditary sensitives. The reverse change can also be brought about experimentally by removing kappa from the bodies of killers, concentrating it in a dense suspension, and exposing sensitive paramecia to the suspension of kappa particles (*15*). The sensitives take up into their cytoplasm one or a few particles of kappa, which multiply and persist in their bodies and in the bodies of their descendants, making hereditary killers of them.

Up to this point, the killer trait seems to be outside the realm of Mendelian genetics; but the divorce is not complete. Kappa cannot multiply or be maintained in a paramecium unless certain genes are present in the nucleus. One main gene, *K,* must be present and at least one other gene, *s*, is involved in a less conspicuous way (*14*).

How does this analysis of the inheritance of the killer trait bear on the Lysenko controversy? In the first place, like other investigations, it demonstrates the existence of material particulate bases of heredity outside the chromosomes in the cytoplasm. Regardless of how rare or how common such particles may turn out to be, regardless of whether they are considered normal or abnormal, regardless of whether they are labeled "plasmagenes," "viruses," or "symbionts," the fact remains that they underlie and determine processes which cannot logically be excluded from the category of inheritance.

The demonstration of inheritance determined by plasmagenes is used by Lysenkoists as support of their contention that the chromosome theory of heredity is not valid. The argument employed is the same as one of those used against the Mendelian 3:1 ratio: any exception to a rule disproves the rule. Thus, if inheritance is sometimes not due to nuclear genes, then, they conclude, it can never be due to nuclear genes. The fact is, on the contrary, that there are two distinct categories of inheritance, Mendelian and non-Mendelian, as has been known for forty years. Further, the plasmagene kappa is actually dependent upon Mendelian genes for its maintenance. The work on plasmagenes serves to show that there are two kinds of genes, nuclear and cytoplasmic; it is therefore merely an addition to, not in any sense a replacement of, neo-Mendelism.

It may be supposed that the demonstration of plasmagenes supports the view of the Lysenkoists that other parts of the cell than the chromosomes are the materials of heredity. Such a conclusion is based, however, on a fundamental misunderstanding of the Lysenkoist view. The Lysenkoists deny the existence of any special substance of heredity and therefore reject the plasmagene along with the nuclear gene. They will not admit that control of any particular hereditary trait is localized in any particles, either in the nucleus or in the cytoplasm. Hence, the demonstration of plasmagenes not only fails to support Lysenkoism, but is at variance with their views.

The second point of contact between the work on killer paramecia and Lysenkoism is with respect to the inheritance of acquired characters. A number of environmental agents can transform killers into sensitives or sensitives into killers and these changes are inherited. Is this the inheritance of acquired characters? For acquired characters to be inherited in *Paramecium,* acquired traits must be transmitted through sexual reproduction. Usually, only a nucleus passes into the mate during conjugation and it does not carry kappa. Under certain conditions, however, not only the migratory pronucleus, but also some cytoplasm passes into the mate during fertilization and then kappa may be carried across in the cytoplasm. Under these conditions acquired changes with respect to the killer trait may be inherited.

Even more instructive in this connection is the behavior of a plasmagene (the so-called "genoid," sigma) in the cytoplasm of the fruit fly *Drosophila* (*8*). Not only is it regularly transmitted by the egg and sometimes also by the sperm, but, more remarkably, it can migrate from body cells to the germ cells, which then pass it on to later generations. Plasmagenes that can migrate from soma to germ cells provide a possible mechanism for the inheritance of acquired characters. But it must be emphasized that such a mechanism is absolutely restricted to the relatively small class of non-Mendelian traits and, moreover, to the fraction of this class which is determined by migratory or "infectious" plasmagenes. So far as present knowledge goes, this fraction is so small that it is usually considered abnormal and migratory plasmagenes are often viewed as infectious viruses.

However, even if migratory plasmagenes should prove to be far commoner than now appears, this will not in the least invalidate neo-Mendelism. The phenomenon constitutes a further discovery about plasmagenes, which (as I pointed out earlier) are but an *addition* to genetics, not a *replacement* of any part of it.

Before leaving the subject of migratory plasmagenes as a possible mechanism for the inheritance of acquired characters, it should be emphasized that the same method used by L'Héritier to demonstrate that the *Drosophila* plasmagene could migrate from soma to germ cells, had been used by Castle and Phillips and by others for Mendelian traits of mammals and other organisms. The method is to transplant ovaries from individuals of one type to individuals of the alternative type and to see whether the eggs from the transplanted ovaries show any effects of having resided in an individual with a different heredity. This is, in effect, the animal equivalent of the Michurin graft hybrid technique. The important point here is that this method shows the complete independence of traits known to be determined by nuclear genes; they are in no way affected by the heredity of the host. Acquired characters are thus not inherited when traits are of Mendelian type, that is, when they belong to the class that includes the overwhelming majority of known hereditary traits.

In sum, the work on kappa in *Paramecium* and on other plasmagenes shows that acquired characters can be inherited if the characters fall in a certain subdivision of the non-Mendelian category. This, however, does not undermine neo-Mendelian genetics, for it deals with an entirely separate category of phenomena.

I turn now to another investigation from our laboratory, one which is still in progress. It deals with antigens, specific chemical substances carried by the paramecia. These result in the immobilization or paralysis of the paramecia when the paramecia are brought into contact with specific complementary substances, called antibodies, obtained in the serum of rabbits immunized against these paramecia. The type of immobilization antigen carried by a paramecium is a hereditary trait and many different strains of paramecia differing in their immobilization antigens are known.

By several environmental means, the paramecia can be transformed so that they replace one kind of hereditary immobilization antigen by another one (*14, 16, 18*). Repeated transformations have yielded as many as eight different hereditary antigenic types from the progeny of one original paramecium. Moreover, by choosing appropriate environmental conditions, it has been possible to *direct* the transformations to one particular antigenic type among the eight possibilities (*16*). As one of the agents used to bring about these transformations is specific immobilizing antiserum which, in high concentration, is capable of killing the paramecia, and as the transformed organisms can be completely resistant to this agent, the transformation response is adaptive, although the adaptation is to an environmental agent seldom or never normally encountered in the life of a paramecium.

The mechanisms involved in the inheritance of the antigenic types are still not fully known. The nuclear genes clearly play a part in this, as is shown when different races are crossbred (*16, 17, 19*). The series of antigenic types producible is different in such different races. The genes control what kinds of antigens can be produced in a race and also the detailed structure of the antigens; in other words, they determine to what types the animals of a given race can be transformed. But the different types within one race are all alike in their genes and these differences are cytoplasmically inherited. Thus far it has been impossible to demonstrate that this cytoplasmic inheritance is by means of plasmagenes; an entirely different and as yet unknown mechanism of cytoplasmic inheritance may be involved. The role of the transforming environmental agents is clearly to bring about shifts from one to another of the several possibilities determined by the nuclear genes.

So far as the bearing on Lysenkoism is concerned, I shall not take the time to discuss again those features of the antigen system which are similar to the killer system already discussed, but shall pass at once to the new features. The first is the relation between environmental effects and nuclear genes. Here the nuclear genes, which Lysenko does not recognize, are the ultimate masters of the situation: the environment can transform only to a type for which the corresponding gene is present—a result which finds no place in Lysenkoism.

But the main new feature of the antigen work is that specifiable environmental conditions can force upon the cells specifically adapted and directed responses which are thereafter inherited through the cytoplasm. These acquired characters are sometimes transmitted to mates in sexual reproduction when massive amounts of the cytoplasm pass across to the mate during conjugation, as happens rarely. Since we have thus far been unable to obtain decisive evidence that the physical basis of this cytoplasmic inheritance is plasmagenic, it is possible that acquired characters in a unicellular organism may be transmitted by a mechanism other than that of an infectious plasmagene.

However, unicellular organisms are in a unique position in relation to the inheritance of acquired characters. Unlike multicellular organisms, they have whatever may correspond to soma and germ plasm within the confines of a single cell; and in many species of unicellular organisms, any cell can function either as a vegetative or a sexual cell. Hence, whatever results are obtained on these creatures by reason of these two unique features should not be extended to multicellular organisms without further evidence.

On the other hand, the results with *Paramecium* do bring out two fundamental facts that are critical for the Lysenkoist views. First is the fact of localization of decisive genetic determinants in different parts of the cell. In the two examples of inheritance of acquired characters, the decisive determinants are localized in the cytoplasm and are never transmitted by the nucleus. Such localization is contrary to Lysenkoism, which holds that each part of the cell—including the chromosomes, and presumably each part of every chromosome—is the material basis of the *entire* heredity of the cell.

Second, changes in the cytoplasm do not bring about corresponding (or any yet detected) changes in the gamete nuclei. Gamete nuclei produced in a cell with altered cytoplasm do not carry or transmit the change in heredity. This is shown not only by the two investigations referred to here, but also by three other investigations in which I have studied acquired characters. According to Lysenko, on the contrary, a genetic change in any region of the cell should be carried and transmitted by any part of the cell. In view of these results on the unicellular *Paramecium*, how much less would one expect to find changes in the body cells of higher organisms transmitted to germ cells not derived from them, particularly to the nuclei of those germ cells.

Our work on *Paramecium* thus yields three main results all of which are in opposition to the claims of the Lysenkoists. First, the examples of cytoplasmic inheritance show that even this is closely tied up with the system of nuclear genes. Second, a special substance of heredity, which Lysenko does not admit, also underlies even some cases of cytoplasmic inheritance. Third, changes in the cytoplasm have no effect on the gamete nuclei.

However, we do find, in the work on cytoplasmic inheritance, evidence for the inheritance of acquired characters, but only when the characters belong to that very small class which is determined by migratory plasmagenes (or viruses) or when the characters occur in unicellular organisms. It is conceivable, but not yet demonstrated, that similar (but not identical) phenomena could occur in plants, because the germ cells arise from various parts of the plant body relatively late in the life history. Since the germ cells would, in this case, be lineally descended from the cells manifesting the acquired trait, the term "inheritance of acquired characters" is strictly speaking not applicable to this hypothetical situation. And it is important to be very clear that, for nearly all hereditary traits in all kinds of organisms—those which are determined by nuclear genes—there is as yet no convincing evidence that acquired changes are ever inherited.

In sum, there is no legitimate scientific ground for the Lysenkoists' rejection of neo-Mendelism and the chromosome theory of heredity. Their ideas are not supported by their own inadequately controlled experiments, and they are contradicted by the controlled experiments of others. Further, recent work on cytoplasmic inheritance, sometimes cited in support of Lysenko, yields results in fundamental opposition to his views. Even the inheritance of acquired characters, which occurs in some of these cases, holds only for a small class of exceptional traits and does not apply at all to the usual gene-controlled traits. The Lysenkoist "new genetics" is thus not scientifically justified.

The Lysenkoists' Response to Criticism

Do the Lysenkoists know the criticisms that have been raised about their experimental work? If so, what have they done about them? The Lysenkoists do know the criticisms that have been raised concerning their experiments; they have been pointed out repeatedly by the Russian geneticists themselves. However, this has not led to repetition of the experiments in such a way as to avoid the most serious errors. Their response to criticism can be best illustrated in their own words:

> . . . bourgeois biologists abroad can console themselves only by saying that Soviet biologists can get easy results from intravarietal crosses of self-pollenaters because the varieties used in Russia are "not pure." However, such a laughable appeal "to the impure" [Russian pun, meaning "to the devil"] when speaking of a good, full, valuable scientific life, is in vain. [Reference *12*, p. 18.]
>
> . . . there are some faithful Morganists who try to deny the facts that overthrow Morganism. They keep in store, as ready answers to all experimental data that disprove their theory, either the general excuse of "impurity" of original stock, or just one word: mutation. [Reference *12*, p. 22.]

No further discussion of impurity is to be found; no citation of controlled experiments; no acknowledgment that they are needed. The mere statement that "impurity" is the usual and general objection is apparently considered to be quite enough to dispose of it.

As scientists, we are all in agreement that the final test of the acceptability of experimental data is independent repetition. We have seen that independent experiments performed outside of Russia (and also many performed in Russia) have failed to confirm the results of the Lysenkoists. To this, the Lysenkoists reply: The proper technique was not employed. Yet they will not specify what the proper techniques are in such a way that others can employ them. One of their own geneticists made this clear during a debate on this subject in Russia in August, 1948. He said:

> I want to make a personal request of Trofim Denisovich [Lysenko]. Trofim Denisovich, instruct your organization to issue a comprehensive manual on how to train plants, on how to alter them. Teach us; we too want to learn, and if your methods prove effective, we will accept them. [Reference *21*, p. 466.]

With this modest and basic request, the rest of the world of science can only join. I therefore challenge the Lysenkoists, as did their own Soviet neo-Mendelist, to provide detailed descriptions of methods so that their assumed revolutionary findings can be independently tested by others. I further challenge them to repeat their own experiments with the controls demanded by their critics and to publish the results with full numerical data so that others can analyze them for statistical significance, even if they themselves refuse to do so. If the future may be judged by the past, neither of these challenges will be accepted.

Standards of Scientific Validity

As scientists we must inquire further as to why such challenges have not been accepted and as to why the same experiments look so different to Lysenkoists and to us. A full discussion of this aspect of the Lysenko controversy is beyond the scope of this paper. It can be found in the little booklet of Hudson and Richens and in the two recent books by Zirkle (*20*) and Huxley (*7*). Those who wish to deduce the answers for themselves from the original sources can readily do so by reading *The Situation in Biological Science* (*21*), a large book containing the official Russian translation into English of the Proceedings of the Lenin Academy of Agricultural Sciences of the USSR, for the meeting held July 31 till August 7, 1948. From these sources it will become evident that the standards of scientific validity employed by the Lysenkoists are entirely different from those accepted elsewhere in the world.

The Lysenkoists, in brief, employ the following standards: (1) appeal to authorities, recognized and approved by them, such as Darwin, Michurin, and Burbank; (2) rejection as heresies views that can be represented as inconsistent with an approved authority; (3) rejection of evidence if the worker can be represented as badly motivated or under disapproved influences, for example, by maintaining that he is a reactionary, an idealist, bourgeois, or a foreigner; (4) testing the validity of a theory by the speed and frequency with which adherents of the theory produce practically useful results.

Not only are these standards of scientific validity, which we consider irrelevant, employed, but our standard of objective evaluation of evidence is expressly abjured. Thus, Y. Zhdanov of the science department of the Central Committee of the Communist Party, in a letter addressed to Stalin, appealed to Lenin as authority for "the danger of falling into objectivism" which Zhdanov confessed as one of his own faults derived from his "regrettable 'university habit' of not hesitating to express my own point of view in a scientific argument" (*7*, p. 228). This he promised to correct.

Of all the scientific standards recognized by the Lysenkoists as valid, perhaps none is more important than agreement with the philosophy of dialectical materialism. In perusing the great debate of August, 1948, it will be noted that *both* sides, the Mendelian geneticists and the Lysenkoists, attempted to show how their views were consistent with dialectical materialism.

The reason is that dialectical materialism is the official philosophy of the Communist Party and the Soviet Government. It is obligatory that scientific work should appear to conform with it, or at least that it shall not be shown to be at odds with it. Ashby (*1*), in his book *Scientist in Russia,* reports that most scientists of the older generation manage in a perfunctory way to appear to conform although they continue really to employ the same scientific standards as we do. The Lysenkoists, on the other hand, have used conformity with dialectical materialism as a powerful means of enlisting support for their own views and for discrediting the work of the Mendelians.

Politics and Science

Through dialectical materialism, science in Russia maintains an intimate and ever threatening contact with politics. This philosophy is the official philosophy of the state and it is supposed to guide science in ways that Lenin and other leading Communists have pointed out. That this connection between politics and science can be disastrous for science is illustrated well by the events recorded in the proceedings of the August 1948 conference to which I have referred. At the close of the conference, Lysenko, president of the Academy, introduced his concluding remarks with the following (*21*, p. 605):

> Comrades, before I pass to my concluding remarks I consider it my duty to make the following statement.
>
> The question is asked in one of the notes handed to me, What is the attitude of the Central Committee of the Party to my report? I answer: The Central Committee of the Party examined my report and approved it. (Stormy applause. Ovation. All rise.)

Towards the end of this speech, Lysenko added (*21*, p. 617):

> The Party and the Government are showing paternal concern for the strengthening and development of the Michurin trend in our science, for the removal of all obstacles to its further progress.

Following this statement, three of Lysenko's opponents, who had argued in defense of what is known as genetics everywhere else in the world, recanted their opposition and pledged support to what had been announced as the doctrine to be supported by the party and the government. Let us examine the reasons given for their recantation. Academician Zhukovsky said the following:

> The speech I made the day before yesterday, at a time when the Central Committee of the Party had (unknown to him) drawn a dividing line between the two trends in biological science, was unworthy of a member of the Communist Party and of a Soviet scientist. [Reference *21*, p. 618.]
>
> I consider it to be my moral duty to be a sincere Michurinist, a sincere Soviet biologist. [Reference *21*, p. 619.]
>
> It has been said here (and the reproach is deserved) that we do not conduct a fight in the press against foreign reactionaries in the field of biological science. I declare

here that I shall conduct that fight, that I attach political importance to it. [Reference *21*, p. 619.]

I take this step today as a Party member, as a sincere member of our Party—that is, honestly. (Applause.) [Reference *21*, p. 620.]

I have not omitted any part of the speech that states a single scientific reason for recanting, or any implication that the decision was based on anything but the one fact that the Communist Party and Government had declared for Lysenkoism.

From the second speech of renunciation, by S. I. Alikhanian, I quote (*21*, p. 62):

From tomorrow on I shall not only myself, in all my scientific activity, try to emancipate myself from the old reactionary Weismann-Morganian views, but shall try to reform and convince all my pupils and comrades.

There is no denying that this will be an extremely difficult and painful process. Many perhaps will not understand this; but then there is nothing to be done—our way and their way will part. It will mean that they cannot appreciate the assistance the Party has rendered us in this radical turn which has taken place in science. . . .

From the third speech of renunciation, by I. M. Polyakov, I quote (*21*, p. 623):

It is necessary to understand the chief and fundamental thing, namely, that our Party has helped us to effect a profound and radical reconstruction of our science, has shown us that the Michurin theory defines the basic line of development of Soviet biological science, and from this we must draw the conclusion and work to promote the Michurin trend.

My quotations need no commentary. They show better than any citation of facts or arguments why neo-Mendelian genetics has disappeared from the Soviet Union. It is strictly a political matter and has nothing to do with scientific evidence as known elsewhere in the world. I urge all who may still be in doubt to read themselves the book which the Soviets have translated and spread abroad. To them it is natural and right that the state or the party should decide what is correct and permissible in science and should root out and suppress all that fails to conform. The Mendelian geneticists who were members of the party had to choose between setting science above the party or the party above science. The latter was their choice, as they clearly set forth in their speeches of renunciation. As they said, it is difficult, but not impossible to readjust their science to suit the will of the party. In view of this, let the Communists of our own country be as truthful and frank as the Communist geneticists of Russia and confess that they support Lysenko because the party supports him; that it is quite irrelevant whether he has or has not given adequate experimental support to his biological pronouncements; that his science must be correct because the party has decided that only his views of biology are consistent with dialectical materialism.

I have yet another quotation to add; it is from *Pravda*, August 27, 1948.

The Praesidium of the Academy of Science and the Bureau of the Biological Department forgot the most important principle in any science—the Party principle. They pegged themselves to a position of political indifference and "objectivity."

In Huxley's excellent, brief, and pointed summing up of the situation (*7*, p. 234):

The issue could not be stated more clearly: Do we want science to continue as the free pursuit of knowledge of and control over nature, or do we want it to become subordinate to political theory and the slave of national governments? It is a crucial question, on which the general public as well as the professional scientist must make up its mind.

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