The Problem of the Inheritance of Acquired Characters

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The Problem of the Inheritance of Acquired Characters

A History of *a priori* and Empirical Methods Used to Find a Solution

[Problema Nasledovaniya Priobremennykh Priznakov. Istoriya Apriornykh i Empiricheskikh Popitok Ee Resheniya]

L.I. BLACHER

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This book is devoted to the problem of the inheritance of acquired characters and the centuries-long controversy over this topic. The views of Lamarck and Darwin are presented in detail. Experiments are described and their results evaluated for investigations concerning the inheritance of the effects of mechanical, thermal, nutritional, and immunological influences. The author gives his own views on the inheritance of acquired behavioral traits, on the influence of the maternal organism bearing a foreign fetus, and on "vegetative hybridization." It is proven that the inheritance of acquired characters is impossible.

This book is intended for biologists of various specialities (geneticists, embryologists, physiologists, zoologists, botanists, and others).

Preface

English translations of secondary texts in the history of science are not common. When undertaken they are normally executed either with the intention of promoting a methodological crusade or out of conviction that the work's coverage is so complete that the value of its wide dissemination outweighs the labor and frustrations of translation. Treatises by Mach, Duhem, Koyré, and more recently by Foulcault and Fleck come to mind as belonging to the first category; the surveys by Taton, Dijksterhuis, and Castiglioni represent the better known examples of the second. Translations of these widely read texts need no apology. The following work by Leonidas Blacher can claim to be neither a methodological breakthrough nor the definitive survey of its subject, yet the editor is convinced that it possesses other features that in combination with its survey nature make it worthy of the historian's attention and warrant the necessary energy of translation and editing. This claim requires a few words of explanation, which might be best introduced by way of a brief account of the translation itself.

The editor's own research interests lie in the domain of the history of late nineteenth and early twentieth century evolutionary biology. As has often been described in secondary works, scientists of the period, almost without exception, accepted biological evolution; they could not, however, agree on the details of the process. Just as they had been in Darwin's day, the mechanisms of and the connection between inheritance and individual variations remained unresolved scientific problems. In 1910, as fifty years earlier, there existed little agreement about how assorted biological factors articulated with one another to bring about the evolution of species. Scientists paraded forth a confusing array of variables, which included external influences, use and disuse, natural selection, geographic isolation, internal growth drives, mutational leaps, and special vital forces. The informed, and not so informed, public kept pace with these quandries and added their own speculations and proclamations about evolutionary mechanisms, which extended far beyond the minimal evidence generally expected of but not always found even in first-rate science. To be sure,

there were important social and philosophical dimensions to the scientific debates, dimensions which emboldened a Samuel Butler, a George Bernard Shaw, or a Henri Bergson to pronounce so confidently upon the mechanisms of evolutionary biology. But it must not be forgotten that the general unsettled state of evolutionary biology itself at the time of the semi-centenary of the *Origin of Species* lent strength through default to uninformed and uncritical claims.

One indicator of the general unsettled state of biology at the turn of the century was the rise to prominence of what is commonly known as the nature-nurture controversy. When it focussed on the development of a single individual, this controversy consisted of debates over the relative contributions to the organism's make-up of heredity and the environment. Were the social misfits, the feeble, the less successful, or simply the foreign born different because of their hereditary constitution or were they so because of their surroundings? When it entailed an explanation for evolution, the nature-nurture controversy revolved about the age-old belief that traits acquired in one lifetime could be transmitted to future generations that need not experience the trait-inducing factors known to the parents. Indeed, between 1880 and 1930 some of the most acrimonious scientific exchanges were directed at defending or refuting the occurrence of the inheritance of acquired characters. As they spilled over into the popular domain both aspects of the nature-nurture controversy took on ideological significance with long-term political implications. There is little doubt that these ideological commitments reinforced, in turn, the scientific claims. Historians find ample evidence of this reciprocal support—better yet, bootstrapping—in the eugenics movement, in social Darwinism, in the tragic career and the subsequent biography of Paul Kammerer, in certain phases of the I.Q. controversy and the socio-biology movement, and, of course, as part of the notorious Lysenko period.

The editor has a particular interest in the historical fortunes of the second aspect of the nature-nurture controversy: The belief in the inheritance of acquired characters. That the belief in such inheritance became a proposition requiring scientific scrutiny after 1880 is part of the history of the emergence of modern genetics. That by 1930 the proposition had, with a few exceptions, failed the tests of science is well documented in the primary literature. But the process of how this particular unchallenged assumption became restated as a scientific claim and how in turn that claim was transformed and dissolved by the leaven of scientific and popular debate is not well described in the general surveys of evolutionary biology. It was with the intent of understanding these processes, i.e., the emergence of a scientific claim, its transformation, and its final rejection that the editor sought guidance from more specialized historical accounts. There exist indeed some substantial ones, particularly by biologists e.g., Ludwig Plate, Emil Guyénot, Richard Semon, and Walter Zimmermann. Their works furnish the scientific details and demonstrate their complexities; they, however, suffer from their narrow focus on the biological issues alone and from the fact that the authors, having been participants in the debates prior to 1930, could not benefit from the perspective afforded us now by the establishment of the evolutionary synthesis of the 1940's and the rise of the central dogma in molecular biology made possible in 1953 by the discovery of the structure of DNA. These scientific advances combined with the increasing sophistication in the writing of the history of science make it essential to re-examine the entire history of the concept of the inheritance of acquired characters.

Just as the editor began to recognize the dimensions of this important problem, Professor Blacher kindly sent him a complementary copy of his own historical study of the subject. Alas, as with most of his western colleagues, Russian literature remains to the editor a terra incognita that lies beyond a forbidding sea of cyrillic symbols. When a friend translated for him the table of contents, it became obvious that any scholar embarked on a thorough study of the concept of the inheritance of acquired characters would need to assess the details of Blacher's book. It was not until the fall of 1976, however, that a small grant from the Indiana University's Office of Research and Development made it possible to employ two graduate students in Russian Studies, Katherine McKinin and Noel Hess. During the next nine months they produced a rough translation of the middle chapters of Blacher's book, chapters which were most directly pertinent to the editor's research program. At first, we intended that these would remain private documents. Soon we realized from the contents that the entire work might be of value to other scholars, as well. A second small grant from Research and Development made it possible for Hess to complete a translation of the entire text, and together, he and the editor reworked the rough translations into publishable form by excising repetitions, clarifying ambiguous passages and verifying quotations and citations.

A number of problems proved particularly irksome in our efforts to produce a smooth English text. Most of Blacher's insights rely heavily on an exacting analysis of the primary texts. This is as it should be in the history of science. In developing his argument, however, Blacher reproduces extended passages from the major participants he discusses; a few of these he borrows from other secondary sources; some he has found in the original texts; many of them, he takes from the standard Russian translations of Western sources. Blacher appropriately and in a thoroughly scholarly manner cites all the sources for the passages he reproduces, but we were left with the dilemma of either translating translations or of justifying quotations with standard Western texts. We soon realized that a

twice translated statement by, let us say, Buffon, Darwin or Kammerer bore only a strange geneological resemblance to the original text. Moreover, if we chose this first option, we would certainly be guilty of putting strange versions of classical texts into circulation and of confounding the uncertainty in an already uncertain and prolix controversy. There seemed no rational alternative but to choose the second and more time-consuming option. We had to go back to the original text, but this goal was easier to state than fulfill. Many of Blacher's citations were unobtainable to Russian editions; moreover, these, as often as not, consisted of collected rather than individual works. The extent and context of the primary passages made it possible for us eventually to locate the great majority of the passages in their original language. Where standard English versions existed of French and German sources, we unabashedly adopted these. When we were forced to provide our own English translations of French and German, we compared Blacher's Russian version with the original and rendered an English translation that we believed did justice to both. We saw the touchstone in the enterprise of verifying and translating primary sources to be the production of a text that other scholars could confidently use as a source and guide to further research. We have been explicit in our footnotes about the origin of all primary passages.

The wealth of primary passages, both Western and Russian, together with Blacher's critical analysis of the exact meaning of the texts, offered one reason why we found this work sufficiently interesting to justify a complete translation. More important, the entire work really constituted a primary source in itself by an important Soviet scientist. A few words about the author's background are therefore in order.

Blacher was born in 1900 in the town of Samara (now Kuybyshev) which lies at the confluence of the Samara and Volga rivers. He received a classical education at school, finishing in 1919; thereupon he attended the medical school of the Second Moscow University. By the time of his graduation in 1925, he had already begun embryological work on sex hormones and secondary sexual characters in the laboratory of Professor Mikhail Mikhayalovich Zavadovsky at the Moscow Zoo. As will be seen in later chapters of this work, Zavadovsky himself had thought extensively about the problem of the inheritance of acquired characters and was to articulate concisely the unlikeliness of such a phenomenon. Blacher also worked at the zoo in Askaniya Nova close to the Crimean Peninsula before returning to the department of General Biology at the Second Moscow University, first as an assistant (1925–1929), then as a lecturer (1929–1933) and finally as professor (1933–1948). During this time his research continued in the area of postembryonic development. Since 1955 he has been associated with the Institute of the History of Science and Technology of the USSR Academy of Sciences. He has published extensively in Russian in

the history of science; his major contributions consist of a two volume *History of Embryology in Russia* (1955-1959), *Historical Sketches on the Problems of Animal Morphology* (1976), and the monograph of which this volume is the translation. He continues to be active in the history of science.

Blacher wrote this work within the context of the immediate post-Lysenko period in Russia. In 1970 indirect and politic corrections of the previous scientific intolerances were still only cautiously presented. All the problems discussed here, whether pertaining to Aristotelian treatises or to the most modern genetics textbooks bear tangentially on the author's own position as a scientist in the Soviet Union. As an embryologist Blacher was less directly involved than the geneticists who contravened against the anti-Mendelian breeding programs of the Ministry of Agriculture. As Blacher's text suggests, perhaps unintentionally, there was however a futility in Lysenko's backward wrenching of the clock in one field of science and not in all. We must not forget that science represents a body of co-ordinated knowledge. Fields articulate with one another, and part of the process of the advance of science consists of the confrontation of the theories and assumptions of one domain with those of another. Accomodation, revision, and improvement result from this jostling at the interface. The field of embryology is constantly interacting with hereditary theory. Indeed, until the twentieth century, they were perceived as one and the same. Development is, after all, the other side of the coin of transmission. Not surprisingly, then, we find that in the post-1900 period many of the tests for the inheritance of acquired characters are of an embryological nature. In fact, much of what sustained the scientific side of the controversy over transmission inheritance, as the phenomenon is sometimes called, arose out of whether an embryological test could arbitrate an issue in genetics. Blacher is keenly aware of the synergistic union of embryology and genetics, and as a practitioner of the former, he necessarily has a theoretical as well as humanistic stake in the fate of the practitioners in the other. His historical work refrains from being a blunt political exposé in support of his unfortunate colleagues. Indeed, Blacher does not refer to the political destruction of Soviet genetics, and Lysenko himself hardly appears in the text. But by reviewing the history of this important scientific concept, Blacher comments forcefully, even though indirectly, upon recent ideological events. He is able to set the historical record straight on many of the scientific efforts to test transmission inheritance, and he leaves no doubt that the techniques and perspective of modern genetics alone can judge the truth or falseness of the neo-Lamarckian claims.

Politicians of all kinds and from all ages have recognized the power in such writing and revision of history. Indeed, no ideology has a monopoly on the misuse of history as a political tool. As Blacher the critical scientist

merges with Blacher the historian, we find him choosing lengthy excerpts from the primary sources in order to expose the degree to which the Lysenko dogma infiltrated the business of writing the history of biology. No one can read the chapters on Darwin, Kovalevsky, or Pavlov without recognizing Blacher's running debate with the editors of the collected works of these scientists. Translations, excisions, editorial comments each had a way of insidiously distorting the historical documents so as to make it appear that these and other scientists passed enthusiastic rather than temporate judgment upon those beliefs later to be promoted by Lysenko and his followers. In this parrying with historical foils when the stakes were of a scientific nature, the reader will find that Blacher follows a tradition already established by fellow biologists, such as Timiriazev, Davitashvili, Filipchenko, and Serebrovskii, turned historians. By writing a history of a scientific controversy, Blacher has quite intentionally written a history of the Soviet histories of that controversy, as well. His book, too, becomes a part of that story and so gains stature in our view as a primary as well as secondary document.

It is worth making a few minor comments about the process of translation. First, although we have added material, we have kept the footnote designation of the original text. This should make it easier for those with access to Blacher's work to compare and use both the original and the translation. Second, Russian names often baffle the uninitiated westerner. Not only are there variant transliterations in common circulation, but rarely do either the scientific texts or secondary sources grace us with anything more than initials for forenames. As economical as such a practice might be for scientific journals, it does violence to an historian's sensitivities to see that most personal part of one's name contracted to a set of impersonal letters for posterity. Wherever possible we have tried to restore forenames as personages first appear in the text. By expanding the index to include these forenames, as well, we hope that that part of the book becomes a more useful tool of reference. We thank both Professors Blacher and Raissa Berg for assisting us in filling out the names and identities of the Russian scientists discussed. With a few obvious exceptions, such as "Dobzhansky," and "Schmalhausen," Noel Hess has chosen to use Method II of J. Thomas Shaw's *Transliteration of Modern Russian for English-Language Publications* (University of Wisconsin Press, 1967) in rendering Russian names into English. We have also adopted the spelling that Blacher prefers for his own name; the Library of Congress, however, prefers "Bliâkher." Finally, we have decided to give a transliteration as well as translation of Russian works. This will not only be useful to scholars who wish to become aware of the originals but serves as a gentle way of encouraging more historians of science to venture upon that cryllic ocean

themselves. The editor can testify that after living with this translation project for four years that the waters are not as forbidding as he once thought. The terra incognita, which he will never reach, certainly contains riches for those who venture further upon these waters.

As editor, I wish to thank Professor Loren Graham for advice about the content of the book and for an initial translation of Blacher's "Introduction." Professor Blacher has kindly responded to a number of lengthy letters seeking clarification and additional information. Professor Raissa Berg, now living in Wisconsin, has also kindly answered my inquiries and has pointed out to me the existence of her and I.I. Kanaev's favorable review of Blacher's book which appeared in the *Journal of General Biology* [Zhurnal Obshchei Biologii] 1973, *34*.

My gratitude is also extended to Dr. Robert Multauf of the Smithsonian Institution who informed me of the Special Foreign Currency Science Information Program, which under the coordination of the National Science Foundation funds translations and publication of important scholarly texts. For many years Multauf had been urging this program to translate works in the history of science and, as it turned out, two of Blacher's books were high on his submitted list. When he learned that the editor and Noel Hess were fully embarked on this monograph, he cancelled the original request for this work to be processed through the above-mentioned program. He then kindly arranged with Mrs. Sharon Sweeting, the translation officer of the Smithsonian Institution Libraries, to intercalate our translation into the process at the publication stage. These details are worth mentioning because they demonstrate how the momentum of government is as inexorable as it is unfathomable. Two years after we had made the above arrangement and after we had completed our own text, Multauf apologetically sent on to us another translation of Blacher's text which had been produced under government contract with the Al-Ahram Center for Scientific Translations in Egypt. This arrived too late to be useful in our own editorial process and is now destined to remain in manuscript form as government property somewhere in the archives of the Smithsonian Institution.

As mentioned above, the two small grants from the Office of Research and Development at Indiana University made it possible for me to employ Katy McKinin and Noel Hess as translators. After the funding came to an end, Hess doggedly pursued the project until its completion. He not only suffered with me through many a rewriting but time and again rechecked our "improved" versions with the original. Besides taking on many of the editorial tasks, he also provided me with a rough translation of the aforementioned Berg-Kanaev review. My thanks also go to Marsha Richmond who proofread the final draft. Finally, no words in any of the languages

used could possibly describe my sense of gratitude to Donna Hazel and Karen Blaisdell who patiently typed and retyped what we produced and reworked and who finally collated text, index, and footnotes.

Bloomington, Indiana
12 March 1981

Frederick B. Churchill

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In memory of my son
Sergei Leonidovich Blacher
20 June 1925–17 December 1969

Author's Introduction

The history of biology contains no more illustrative example of a centuries-long controversy than the disputes over the inheritance or noninheritance of acquired characters.

The question of the inheritance of acquired characters could still be considered an authentic general biological problem if we had not by now identified with a degree of confidence the true mechanisms of evolution. More than a hundred years ago, however, it became clear that we could not give equal credence to both the Lamarckian idea of evolution as a result of direct adaptation and the Darwinian doctrine of evolution by means of natural selection, that is the doctrine of the survival of the fittest from among all the forms that spontaneously arise. The acceptance of direct adaptation was equivalent to the belief that organisms responded to the actions of the environment with purposive, adaptive, and at the same time, hereditary changes. By accepting this, there developed the conviction that the inheritance of acquired characters was not only possible but necessary. The modern theory of evolution, which is a synthesis of classical Darwinism and advances in genetics, has rendered superfluous the proposition that progeny inherit adaptive changes which arise in their parents through the direct action of the environment. Testing the case for inheritance of acquired characters has thus lost all significance for the establishment of the materialistic theory of evolution. Nonetheless, opponents of Darwinism, the representatives of various Lamarckian tendencies, until recently have continued their attempts to establish the theoretical possibility and to prove empirically that acquired characters are inherited. For a long time attempts were made to resolve this issue without rigorously defining the very concept of "the inheritance of acquired characters." But any question which is posed becomes a truly scientific problem only when the concepts needed for its solution have been defined. The persuasiveness of arguments in favor of the inheritance of acquired changes can be evaluated only when one has precisely defined what would constitute the true inheritance of acquired characters.

We can call acquired characters any changes in an organism which due to the direct or indirect influence of changed external conditions appear at any stage of its individual development. For proof of inheritance of such

characters it is necessary to show that they are reproduced in progeny which have developed under the initial ("normal") conditions and that the inheritance of acquired characters is subject to the same regularities as is the inheritance of inborn characters. One must rigorously differentiate an acquired change from a mutation, i.e., a genotypical change in one or both parents, which themselves preserve the initial, unchanged character.

In short, to prove the inheritance of an acquired character, it is necessary to show that the parents acquired the new character and did not inherit it, and that their progeny inherited the changed character and did not acquire it in the course of their individual lives.

A discussion of the question of inheritance of acquired characters also requires a thorough knowledge of evolutionary theory, genetics, cytology, and biochemistry. Nevertheless, the people who have considered themselves qualified to speak out on this issue have included not only biologists of various specialities, but physicians, animal breeders and agronomists, philosophers, psychologists, pedagogues, sociologists, jurists, theologians, sportsmen, publicists and belletrists. The latter presented their own views as well as those of others in their literary works. With the exception of the biologists and occasionally medical and agricultural personnel who used arguments that could be subjected to scientific criticism, the representatives of all the other areas of science and literature expressed opinions devoid of cognitive value, since *a priori* assertions were not supported by convincing arguments.

A source of constant misunderstanding in discussions on this topic has been the confusion between two distinct issues: the truly scientific problem of the relationship between the hereditarily conditioned potentialities of an organism and the conditions of the environment; and the problem of the inheritance of acquired characters. The second of these issues only appears to be organically connected with the first. If the first issue is schematically expressed as a dichotomy: ectogenesis versus autogenesis, then it is easy to show that an *a priori* positive answer to the question of the inheritance of acquired characters does not argue for ectogenesis and, equally, a negative answer does not argue for autogenesis. Nevertheless, for a long time there was a widespread conviction that there existed an inseparable connection between ectogenesis and the acceptance of the inheritance of acquired characters, and similarly between autogenesis and its denial. The conviction was a result of a lack of understanding of the qualitative difference between changes in the individual, changes arising under the direct action of the environment, and evolutionary changes embracing the totality of individuals and also depending directly (mutations) or indirectly (natural selection) on the environment.

External influences evoke in an individual morphological or functional changes that can be either harmful, indifferent, or adaptive, that is, assuring its survival. The adaptive character of individual changes is either simply fortuitous or a result of the previous natural selection of forms that are able to react adaptively to the given influence. In either event, individual changes are not inherited because their appearance is not accompanied by change of hereditary information that would guarantee the appearance of a corresponding change in subsequent generations. If the external agent reaches the sex cells and is capable of changing the hereditary information therein, then the progeny which develop from these sex cells will, in the course of an indefinite number of generations, be changed. The probability of their survival depends on the character of the mutational changes, which may or may not be adaptive to the conditions of the habitat. If the mutational change is compatible with survival but its phenotypic expression does not confer an appreciable advantage over the initial character in the population, then the mutation will be preserved in a fairly stable proportion of the population. Its incidence will increase only when the conditions of the environment change in such a way that it becomes useful. The individual in whose sex cells the hereditary information changed—that is, the progenitor of a mutant generation—does not itself change or, if it changes, does not as a rule acquire those characters which will be inherent in its progeny. Consequently, in this case involving the appearance of hereditary changes, which are the material of evolution, there is nothing present which could be called an acquired character.

This is the modern understanding of this question. Nonetheless, an historical analysis of the discussion of the inheritance of acquired characters, including a critical examination of evidence relating to the question, is not without current interest since certain authors have, up to very recent times, tried to defend the possibility of the inheritance of changes acquired in the course of individual life. Such authors as Wintrebert, Bourdier, and Fothergill have urged the possibility of changes in the hereditary substance that can guarantee the appearance in progeny of characters that arose in the parents under the direct influence of the environment or the changed function of this or that organ.

All the aforesaid justifies the writing of a small book illuminating the history of the discussions which led to the establishment of the *law of the noninheritance of acquired characters*.

The author expresses his sincere gratitude to the members of the Sector for the History of the Biological Sciences of the Institute of the History of Science and Technology of the Academy of Sciences of the USSR for comments during discussion of the manuscript, including his scientific colleagues N.A. Grigorian and E.N. Mirzoian, to F.Kh. Bakhteev and V.L. Merkulov for identifying literary sources, and to S. Ia. Kraevoi, L.V. Krushinskii, and especially B.L. Astaurov for valuable advice.

CHAPTER 1

Antiquity and the Middle Ages

Are traits that arise in an organism during its individual lifetime inherited or not? The origins of disagreement over this question are lost in the depths of time. The belief that acquired traits could be transmitted to progeny was based on poetic legends, religious myths, and unverified reports drawn from everyday life. Even in antiquity this belief met with skepticism.

Conway Zirkle made a detailed study of the early history of views on the inheritance of acquired traits,[1] in which he traced the evolution of this problem up to the middle of the nineteenth century. He compared ideas on the question of inheritance of characters acquired after birth with the recurrent view that the seed originates in all parts of the body. Such a mechanism served for centuries as an explanation for the inheritance of acquired changes. In using the term "pangenesis," Zirkle followed Darwin, who revived this doctrine in his work on *Variation of Plants and Animals Under Cultivation*.

If we discount Empedocles, who proposed that the division of the vertebral column into separate segments resulted from numerous fractures of the column due to its continuous bending,[2] then the first authors we should mention who tried to establish the possibility of the inheritance of acquired changes are Hippocrates and the assorted anonymous authors of the fifth century B.C. Hippocratic Corpus. They discussed this issue in two books of the corpus. In *Airs, Waters, Places,* they claimed that among peoples who bound their children's heads to give the skull an elongated form, the new head shape became hereditary. Hippocrates assumed that the altered structure gave off altered semen. He wrote, "Originally custom was chiefly responsible for the length of the head, but now custom is reinforced by nature. . . . Custom originally so acted that through force such a nature came into being; but as time went on the process became natural, so that custom no longer exercised compulsion. For the seed

[1] Conway Zirkle, "The Early History of the Idea of the Inheritance of Acquired Characters and of Pangenesis," *Trans. Amer. Philos. Soc.*, 1946, *35*: 91–151.

[2] Henry Fairfield Osborn, *From the Greeks to Darwin: The Development of the Evolution Idea Through Twenty-four Centuries* (2nd ed.; New York-London, 1929), p. 56.

comes from all parts of the body, healthy seed from healthy parts, diseased seed from diseased parts."[3] The idea of pangenesis, that is, the formation of the seed from substances collected from the entire body, was repeated in another book of the Hippocratic Corpus, *On Generation*. "I say that the sperm comes from the whole body, from the solid parts as well as from the soft parts and from all the humors which are in the body."[4] "If one of the parents contributes more for resemblance and from more parts of the body, then the offspring will resemble that parent in more parts."[5]

Hippocrates did not consider that injuries were necessarily inherited. He wrote, "It usually happens that the children of crippled people are born healthy, because the crippled person has the same complement as a healthy person. But when the infirmity affects the humors from which the semen is made and the four humors which are usually naturally present furnish semen which is defective and weak with respect to the crippled part, then it does not seem surprising to me that the children are crippled in the same parts as the father."[6]

Aristotle spoke out against the Hippocratic theory of pangenesis. Without naming Hippocrates but certainly with him in mind, Aristotle wrote, "There are some who assert that the semen is drawn from the whole of the body. . . . And these opinions are plausibly supported by such evidences as that children are born with a likeness to their parents, not only in congenital but also in acquired characteristics; for before now when the parents have had scars, the children have been born with a mark in the form of a scar in the same place."[7] "Upon examination of the subject, however, the opposite seems more likely to be true; indeed, it is not difficult to refute these arguments. . . . First of all, then, resemblance is no proof that the semen is drawn from the whole of the body, because children resemble their parents in voice, nails, and hair and even in the way they move; but nothing whatever is drawn from these things."[8] Further on he wrote: "it is plain that the substance which is drawn from the various parts of the parent has no right to the same name as those parts—we may not call that 'blood' which is drawn from the parents' blood, and the same with flesh. This means that the offspring's blood is formed out of something

[3] Hippocrates, *Izbrannye Knigi* [*Selected Books*], trans. V.I. Rudnev, ed., introduction and annotations. V.P. Karpov (Moscow, 1936), p. 294 [quoted in Zirkle (n. 1), pp. 93–94. See also, *Airs, Waters, Places,* trans. W.H.S. Jones in *Hippocrates* Vol. I (Loeb Classical Library), Cambridge, Mass.: Harvard University, 1957, pp. 111].

[4] *Ibid.*, p. 226.

[5] *Ibid.*, p. 229.

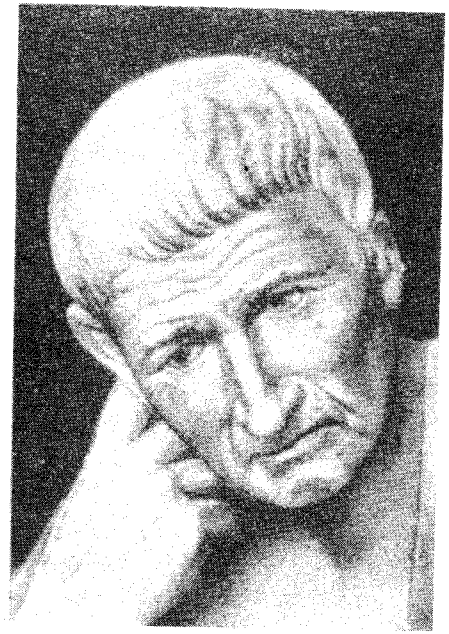
[6] *Ibid.*, p. 231.

[7] Aristotle, *O vozniknovenii zhivotnykh*, trans. V.P. Karpov (Moscow-Leningrad, 1940), I, 17, 722a, p. 66 [quotations follow *Generation of Animals*, trans. A.L. Peck (Loeb Classical Library), Cambridge, Mass.: Harvard University Press, 1953, 721b and 722a].

[8] *Ibid.*, I. 18, 722b, p. 67.

which is other than blood, and if so, then the cause of its resemblance will not be due to the semen's being drawn from all the parts of the parent's body, as the supporters of this theory assert. . . . Again, how are these parts which were drawn from the whole of the parent's body going to grow?"[9] These last words are especially noteworthy. They pose the question, though not well formulated, of how particles from the changed organ "grow" during development of the offspring so that they form an organ which is altered in turn just as it was in the parent. Thus, we see that Aristotle was aware of the difficulties involved in assuming that changes in the traits of parents can induce changes in the progeny of a similar sort.

The polemics between Aristotle and the Hippocratics show that opposing views concerning the inheritability of variations caused by external influences were current almost 2500 years ago.



Aristotle
(384–322 B.C.)

The correlation between the different races of man and the different climates is also an ancient one. Around the beginning of our Era (A.D.) it was supposed that the color of a man's skin depended on the action of the sun's rays and that changes in skin color were inherited. In particular, this

[9] *Ibid.*, 18, 723a, p. 69.

belief was recounted in the legend of Phaëthon by Ovid, who drew on a widely held belief. When the sun chariot, driven by Phaëthon, approached too close to Earth, "they believe that then, because their blood was drawn by the heat so quickly to the surface of their bodies, the Ethopian people acquired their blackness."[10] Similar views were expressed much later—in the second half of the eighteenth century (see chapter 2).

In general, in the late ancient period no significant interest was shown in the question of inheritance of acquired traits. The philosopher-poet Lucretius apparently did not concern himself at all with this problem. Samuil L'vovich Sobol' noted that in Lucretius's poem *On the Nature of Things,* "there is no evidence that Lucretius shared the rather widely held view of the ancients about the hereditary transmission of acquired traits."[11] Zirkle made the same assessment of Lucretius's attitude toward this problem.

Likewise, in the Middle Ages there were no well-formulated views concerning the possibility of inheritance of acquired variation, despite a reverence toward the "father of medicine," Hippocrates, and even despite the fact that in biblical legends belief in the inheritance of acquired characters is supported by the doctrine of original sin and by other examples.

The teleological world view predominant in the Middle Ages did not extinguish the confrontation between diametrically opposite views concerning the inheritance of acquired characters. In the thirteenth century Vincent de Beauvais rejected the inheritance of injuries since, in his opinion, nature avoided imperfection and tried to correct defects in some parts of the body at the expense of material from other parts.[12] De Beauvais's contemporary, Roger Bacon, on the other hand, was certain that injuries to the organism were inherited and became more pronounced from generation to generation, as happened when father, son, and grandson "neglected the rules of health."[13] Other men of the thirteenth century, such as Albertus Magnus and Thomas Aquinas held views of the same kind, based on ancient authorities.

[10] Publius Ovidius Naso, *Metamorfozy* [*Metamorphosis*], trans. S.V. Shervinskii (Leningrad, 1937), book II (235–36), p. 30.

[11] Samuil L'vovich Sobol', "Problemy obshchei biologii v poeme Ludretsiia" ["Problems of General Biology in Lucretius' Poem"], in *O prirode veshchei* [*On the Nature of Things*], by Lucretius, vol. II: Articles and Commentary (1947), 67.

[12] Vincent de Beauvais, *Speculum Naturale,* Bk 32, ch. 11.

[13] Roger Bacon, *Opus Majus,* pars IV, Cap. XII, 1268. Works by de Beauvais and Bacon are quoted according to Zirkle (see n. 1).

CHAPTER 2

From the Renaissance to Lamarck

Among physicians and anatomists of the sixteenth century there was no single opinion as to the inheritance of the results of injury and other external influences. In his anatomical treatise, *De Fabrica,* Andreas Vesalius cited the example that Hippocrates had introduced of the inheritance of the altered skull shape that resulted from head binding.[1] We need not conclude, however, that Vesalius himself agreed with such reasoning. In the same period Girolamo Cardano explained that the unique head shape of American Indians was due to an hereditary transmission of the results of mechanical squeezing. "This artificially created form grew into a natural one. For the offspring that had been born from those whose heads had been pressed between plates from the beginning and in turn had had their own heads shaped immediately, had offspring which had contracted a similar form."[2]

Authors of the seventeenth century often cited examples which, in their opinion, argued for the inheritance of injuries. In his work elaborately entitled *Two treatises, in one of which, the Nature of Bodies, in the other, the Nature of Man's Soule is looked into, in way of discovery of the immortality of Reasonable Soules,* Kenelm Digby told of a cat "that had its tail cut off when it was very young: which cat happening afterwards to have young ones, half the kitlings proved without tails, and the other half had them in an ordinary manner."[3] Nathaniel Highmore depended on the same sort of isolated examples. "I saw a Mungril Bitch, that had her tail cut close to her body almost, whose Whelps were half without tails, and half with tails: the next year following, she brought them forth all with long tails."[4] On the other hand, Highmore also noted that among spaniels, whose tails are regularly cut off, the puppies are always born with tails. John Ray, in his *Wisdom of God Manifested in the Work of Creation,* expressed the view "the Seed of Animals is admirably qualified to be

[1] Andreas Vesalius *O stroenii chelovecheskogo tela* [*De Corporis Humani Fabrica*] (1543), trans. V.N. Ternovskii (1950), vol. I, p. 81 [see Zirkle (chap. 1, n. 1), p. 97].

[2] Girolamo Cardano, *De Rerum Varietate* (1557), Bk 8, ch. 43.

[3] Works of Cardano and Kenelm Digby are quoted according to Zirkle, *op. cit.,* pp. 98-102.

[4] Nathaniel Highmore, *History of Generation* (1651) [see Zirkle, *Ibid.,* pp. 102-103].

fashion'd and form'd by the *Plastick Nature* into an organical Body, containing the Principles or component particles of all the several homogenous Parts thereof. . . ."[5] It seems that this would guarantee the inheritance of any injury. But Ray spoke cautiously on this point. In his opinion offspring only sometimes inherited the defects and imperfections of their parents.

In the eighteenth century there began to appear in print more and more reports and simply unsubstantiated assertions about the inheritance of acquired traits. In particular, the origin of racial differences in man was once more attributed to climatic influences. It was thought that this influence had a cumulative effect over the generations. In complete seriousness certain authors repeated the view, which Ovid had mentioned long before, that the black skin color of Negroes is the result of burning by the sun. Thus John Mitchell, in "An essay upon the causes of different colors of people in different climates," asserted that skin color is conditioned by the environment, which can, over several generations, create distinct racial differences. "Regarding the remote causes of the Negroes' skin color," he wrote, "it is usually accepted, though not universally, that the action of the sun in hot lands was the principal, if not the only, causative factor. . . . However, it is difficult, if not impossible, to discover or prove how . . . blackness is evoked by the activity of the sun, though it is easy to show that the sun makes skin thicker and tougher . . . and we consider thickness and toughness of skin to be the immediate cause of its black or brown hue."[6]

Pierre de Maupertuis thought that the basis of racial differences in people was in the properties of their seminal fluids; actualization of these properties depended on the influence of climate and food. He wrote, "It seems that the heat of the torrid zone is more suited for the formation of the particles which render the skin black, than for those which make it white; and I do not know whether this can be obtained by the influence of the climate or of diet after many centuries."[7] Maupertuis very clearly associated the idea of inheritance of acquired traits with the principle of pangenesis. He considered the idea well founded that "in each seed there are parts destined to form the heart, head, entrails, hands, legs."[8] In another passage Maupertuis posed the question: "How, in the seed of any animal, do the characteristic parts of that animal form? It would be a daring proposal, though not beyond reason, that each part forms its own new rudi-

[5] John Ray, *The Wisdom of God Manifested in the Works of Creation* (1691). [Excerpts from Highmore and Ray are quoted according to Zirkle, *ibid.,* pp. 104-105].

[6] John Mitchell, "An Essay Upon the Causes of Different Colors of People in Different Climates," *Phil. Trans. Roy. Soc. London,* 1744, *43:* 103-150.

[7] Pierre Louis Moreau de Maupertuis, "Variétés dans l'espèce humaine," *Vénus Physique* (7th ed.; Geneva, 1780), part II, pp. 137-138 [quotation according to Zirkle, *op. cit.,* p. 106].

[8] *Ibid.,* p. 97.

ment. This could be verified by an experiment in which animals are maimed over many generations. Perhaps this would result in the injured parts gradually diminishing or finally disappearing altogether.''[9] Maupertuis advised philosophers to verify whether artificially produced features in animals are retained in succeeding generations, in particular, ''whether the tail and ears diminish or disappear when they are cut off generation after generation.''[10]

Benoît de Maillet, in his book entitled *Telliamed* (his surname spelled backwards), asserted that aquatic forms could be transformed into air-breathing forms over a single generation. He believed that the new traits, which arose under the influence of the environment, were transmitted to succeeding generations.[11]

Comte de Buffon also shared the belief that the results of injury and of the use of organs are inherited. In contrast to Maupertuis, who confined himself to speculating and advising ''philosophers'' to conduct the corresponding experiments, Buffon confidently stated, ''Dogs which have had their tails and ears cut for a few generations transmit those defects wholly, or partly, to their descendants.''[12] To explain the presence of calluses on the chest and on the knees of camels, Buffon said that by loading them with heavy burdens, men forced camels, over many generations, to fall to their knees or lie down, and that the calluses that resulted from friction against the ground must have become hereditary.[13] Buffon believed that the influence of food and climate also caused inheritable changes in animals and man. In Buffon's words, the dog is ''hairless in the hottest lands, covered with thick, tough fur in northern lands, and adorned with a beautiful silken coat in Spain and Syria, where the mild temperature changes the fur of most animals to a silken form.''[14] Buffon, like Maupertuis, attributed the origin of the Negro's black skin color to the action of the sun's rays. ''It always seemed to me,'' he wrote, ''that the same factor that causes sunburn when we stay outdoors and are subject to the sun's heat, causes Spaniards to be darker than Frenchmen, Moors to be still darker-skinned, and Negroes to be darkest. We shall not, however, inquire here into how that factor acts, but simply rest assured that it does act and that its in-

[9] *Ibid.*, pp. 134-135.

[10] *Ibid.*, p. 138.

[11] Benoit de Maillet, ''Telliamed, ou Entretiens d'un philosophe indien avec missionaire françois sur la diminution de la Mer, la formation de la Terre, l'origine de l'Homme, etc.'' (1749). Quoted according to Valezian Viktorovich Lunkevich, *Ot Geraklita do Darvina* [*From Heracles To Darwin*] (Moscow, 1960), vol. II, pp. 169-72 [translation according to Zirkle, *op. cit.*, p. 108].

[12] Georges Leclerc Comte de Buffon, *Oeuvres Philosophiques,* ed. J. Piveteau (Paris, 1954), p. 397.

[13] *Ibid.*, p. 398.

[14] *Ibid.*, p. 397.

fluence is more noticeable the longer and more intensely it acts.''[15] In another passage Buffon simply stated that ''the color of skin, hair, and eyes varies only under the influence of climate.''[16]

Peter Camper, while citing Buffon, expressed a similar point of view. In a public lecture, ''On the origin of the color of Negroes,'' delivered in Gröningen in 1764, he said ''Whether Adam was created brown, tawny, black, or white it is always necessary to admit that his descendents, from the moment that they were dispersed on the surface of the earth, altered their traits and their color according to the climate which they were going to inhabit, the food with which they nourished themselves and the illnesses with which they were attacked. Accidental causes must have also contributed by heritage, as one still sees daily.''[17]

Charles Bonnet disagreed with Buffon's statement concerning inheritance of defects in the ears and tail of dogs. He presented his doubts in a letter to Lazarro Spallanzani. Having cited Buffon's statement about the transmission of injuries in dogs, Bonnet pointed out that Buffon ''enters into no detail thereon, and does not say how he is sure of this. . . . You see this is directly opposed to what I advance, Article 337 of *Organized Bodies.* But English Horses whose tails have been cut for two centuries, do they not refute M. de Buffon and render suspicious the fact that he states as certain?''[18] Bonnet had in mind his composition ''Considerations sur les corps organises,'' where the following passage is found: ''I am not at all surprised that M. de Buffon has believed in this race of dogs deprived of their tails. It is in accord with his ideas of generation. He has imagined that each integral part of the individual generated is composed of interior molds (moules intérieux) which fashion the organic molecules. The amputation of the tail of a dog would involve the amputation of the mold of the tail. But for two centuries the English have cut the tails of their horses, yet these are still born with their tails. For a still longer period, the Hottentots have cut out one testicle from their babies yet all the Hottentots are born with two testicles. A blind man has offspring with two eyes, a one-armed man has infants with two hands.''[19]

Johann Friedrich Blumenbach was likewise unconvinced of the possibility of the inheritance of injuries, and in his *De generis humani varietate*

[15] Georges Leclerc Comte de Buffon, *Histoire naturelle générale et particuliere* (Paris, 1749), vol. III, pp. 525-526, ''Histoire naturelle de l'homme.''

[16] Buffon, *Oeuvres Philosophiques,* p. 395.

[17] Peter Camper, ''De l'origine et de couleur des nègres,'' *Oeuvres,* vol. II (Paris, 1803), pp. 474-475 [quotation according to Zirkle, *op, cit.*, p. 108].

[18] Charles Bonnet, Eighth letter to Spallanzani 9 January 1768, in *Oeuvres d'histoire naturelle et de philosophie,* vol. V, pt. II (Neuchatel, 1781), p. 52 [quotation according to Zirkle, *ibid.*, p. 108].

[19] Charles Bonnet, ''Considerations sur les corps organisés,'' *Oeuvres,* vol. III (1779), p. 461, footnote [quotation according to Zirkle, *ibid.*, p. 107].

nativa, he thought it necessary to include a special section with the suggestive title, *Problem proposed. Can mutilations and other artifices give a commencement to native varieties of animals?* "It is disputed," he went on to state, "whether deformities or mutilations, effected upon animals either by accident or advisedly, especially in those cases where they have been repeated for many series of generations, can at length in progress of time terminate in a sort of second nature, so that what before was done by art now degenerates into a congenital conformation. Some have asserted this, whilst others on the contrary have denied it. Those who are for the affirmative point to the examples of the young of different kinds of animals, dogs and cats for example, which are born without tails or ears after those parts have been cut off from their parents, as is proved by credible witnesses. And of boys among circumcised nations who are frequently born naturally *appellae;* and of scars which parents bear from wounds, whose marks afterwards are congenital in the infants."[20] Blumenbach remarked that people would not unwisely reject this opinion and would oppose it with the alternative view that the coincidental changes on parents and children should be attributed to chance.

In reference to *Sketches in the History of Man,* a treatise by Henry Home, known as Lord Kames, Zirkle commented that this author was one of the very few who were sure that acquired traits were not inherited. According to Kames, "Those who ascribe all to the sun, ought to consider how little probable it is, that the colour it impresses on the parents should be communicated to their infant children, who never saw the sun. . . . . Let a European for years expose himself to the sun in a hot climate, till he is quite brown, his children will nevertheless have the same complexion with those in Europe."[21a]

The voices of individual skeptics who, in the eighteenth century, cast doubt on the inheritance of acquired traits were drowned out by the almost universal acceptance of the possibility of transmission of such traits.

Belief in the inheritance of acquired characters rested on the idea of primacy of function over form. As early as Aristotle it was thought that activity, function, or spirit forms the essence of living bodies. "The term 'nature' is used—rightly—in two senses: (a) meaning 'matter,' and (b) meaning 'essence' (the latter including both the 'Efficient' Cause and the 'End'). It is, of course, in this latter sense that the entire Soul or some part of it is the 'nature' of a living creature. Hence on this score especially it should be the duty of the student of Natural science to deal with Soul in preference to matter, inasmuch as it is the Soul that enables the matter to

[20] Johann Friedrich Blumenbach, *De generis humani varietate nativa* (3rd ed.; Göttingen, 1795), pp. 106–107 [quotation according to Zirkle, *ibid.*, p. 110].

[21a] Lord Kames (Henry Home), *Sketches in the History of Man* (Edinburgh: 1774), p. 13 [quotation according to Zirkle, *ibid.*, p. 109].

'be the nature' of an animal (that is, *potentially,* in the same way as a piece of wood 'is' a bed or a stool) rather than the matter which enables the Soul to do so."[21b] And in another passage: "The body exists for the sake of the soul, and the parts of the body for the sake of those functions to which they are naturally adapted."[22]

One of the first to express the idea that the structure of organs depends on their needs, efforts, and exercise, in accordance with Aristotle's idea of the primacy of function over form, was Denis Diderot, in his works *Le reve de d'Alembert* and *Éléments de physiologie.* In Diderot's story Dr. Bordeu, commenting on d'Alembert's dream, speaks cautiously at first. "He is right: organs produce needs and, conversely, needs produce organs."[23] The idea is later expanded: "Organization defines functions and needs. Sometimes needs influence organization; this influence may be so great that it gives rise to organs, and it always changes them."[24] But "Dr. Bordeu" is much more inclined to assume the dependence of an organ's structure on its function than the converse:

> "Dr. Bordeu: I saw how from two stumps over time there grew two arms.
>
> Mle. Lespinass de l'Espinasse: You're lying.
>
> Dr. Bordeu: That's right. But I saw how in the absence of arms the shoulder blades began to elongate, to move like claws, and to be transformed into rudiments of arms.
>
> Mle. de l'Espinasse: What nonsense!
>
> Dr. Bordeu: It's a fact. Assume a number of armless generations, assume unrelenting efforts, and you will see how both extremities grow longer and longer, anchor themselves to the spine, stretch forward, develop fingers, and become arms. Their original structure changes or is perfected by necessity and habitual function."[25]

Diderot also accepted the inheritability of mechanical injuries. He wrote, "I am ready to believe that if over a long period the arms were severed in a series of generations, an armless race would result."[26]

[21b] Aristotle, *O chastiakh zhivotnykh,* trans. V.P. Karpov (Moscow, 1937), first book (A), I, 641a, p. 39 [*Parts of Animals,* trans. A.L. Peck (The Loeb Classical Library), Cambridge, Mass.: Harvard Univ. Press, 1955].

[22] *Ibid.,* Bk I, 645b, p. 51. Commenting on this passage, V.P. Karpov wrote: "I would like to call attention to . . . the fact of his unreserved assertion of the priority of action. Aristotle thought that, as we would say today, function determines form" (p. 185).

[23] Denis Diderot, "Son Dalambera" ["Le reve de d'Alembert"] (1769), *Izbr. soch.* [*Selected Works*], vol. I (Moscow, 1926), p. 165.

[24] Denis Diderot, "Elementy fiziologii" ["Elements de physiologie"] (1774–1780; first published in 1875), *Sobr. soch.* [*Collected Works*], vol. II (Moscow, 1935), p. 433.

[25] Diderot (see n. 23), p. 165.

[26] Diderot (see n. 24), p. 526.

Valezian Viktorovich Lunkevich pointed out that this statement is interesting as evidence of Diderot's thoughts on the inheritance of acquired traits, which "to this day remains one of the unresolved problems of biology."[27]

At the end of the eighteenth century Erasmus Darwin wrote about the inheritance of new variations and about the dependence of an organ's structure on its functions which answer the biological needs. "All animals undergo perpetual transformations; which are in part produced by their own exertions . . . and many of these acquired forms or propensities are transmitted to their posterity."[28] Citing this passage from *Zoonomia,* Henry Fairfield Osborn observed that Erasmus Darwin gave the first clear and definite formulation of the theory of transmission of acquired traits as one of the causes of evolution.[29]

[27] Lunkevich (see n. 11). Ivan Mikhailovich Poliakov, commentator on the posthumous edition of Lunkevich's book, felt it necessary to express his disagreement with this cautious statement. In his opinion, "the question of the inheritance of acquired traits has been answered in the affirmative" (p. 50). Poliakov's statement was not accompanied by factual proof, and it was in contradiction with his other statements on this question (see chapter 3).

[28] Erasmus Darwin, "Zoonomia or Laws of Organic Life" (London, 1794). Quoted according to Henry Fairfield Osborn, *From the Greeks To Darwin: The Development of the Evolution Idea Through Twenty-four Centuries* (2nd ed.; New York-London, 1929).

[29] Osborn (see n. 28), p. 209.

CHAPTER 3

From Lamarck to Darwin: The Relationship between the Hypothesis of Inheritance of Acquired Characters and the Concept of Evolution

In the eighteenth century de Maillet, Buffon, Diderot, Erasmus Darwin, and other authors variously expressed the concept that change in living organisms is dependent on the conditions of those organisms' existence. They also proposed that such change is inheritable. Their views, however, were not presented as generalized formulae, so we cannot justify calling them evolutionary theories. Historians of biology can only find hints of such a concept in these early views.[1] It was Jean Baptiste Lamarck, whose work spanned the eighteenth and nineteenth centuries, who first formulated a complete, internally coherent theory of evolution. He drew together the many views of inheritable changes caused by the intensity of organ function or the direct influence of the environment.

As early as his "Introductory Lecture to a Course on Zoology," presented in 1800, Lamarck spoke of the "favorable circumstances" which nature "requires and which she continues to employ day after day in order to modify her creations." As examples of such circumstances Lamarck listed the influences of "climate, temperature range of the atmosphere and the whole environment, conditions of the habitat, habits, movements, and actions, as well as manner of living, self-preservation, self-defense, and reproduction. As the result of these various influences, abilities expand, are strengthened through exercise, and become diversified thanks to new long-term habits. Imperceptibly the structure, the composition, in a word, the nature and condition of body parts and organs are subjected to these various influences, and the results of the influences are transmitted to future generations by heredity."[2]

In a similar lecture given in 1802, Lamarck first clearly formulated the idea of the primacy of function and the dependence of organ structure on

[1] Such, for example, was Osborn's opinion of the views of Erasmus Darwin (see preceding chapter).

[2] Jean Baptiste Lamarck, *Izbrannye proizvedeniia v dvukh tomakh* [*Selected Works in Two Volumes*], ed. I.M. Poliakov and N.I. Kuzhdin (Moscow, 1955), vol. I, p. 16 [quotations from Lamarck follow Blacher's text unless otherwise stated].

organ function: "It was not the organs, that is, the nature and form of parts of an animal's body which conditioned the animal's habits and special inherent abilities. On the contrary, it was the animal's life style and the circumstances in which its progenitors existed that, with the passage of time, gave form to the animal's body, determined the number and composition of its organs, and therefore, its abilities." [3]

Lamarck stated this position in a more definitive form in a lecture given in 1806, during which he pointed out the significance of this dependence for evolution: "In animals, a more frequent and prolonged use of a given organ gradually strengthens that organ, develops it, enlarges it, and gives it strength in proportion to the duration of use, whereas constant lack of exercise of a given organ insensibly weakens and destroys it, gradually diminishes its ability to function, and ultimately leads to its disappearance." [4] This formulation was repeated word for word in *Zoological Philosophy* (1809) as the First Law of the transformation of species. [5] There, however, Lamarck added that he was referring to those animals which had not achieved the limit of their development. In the 1806 lecture he continued, "Everything that nature causes individuals of a race to acquire or lose as a consequence of the continuous influence of the environment in which the race lives over a sufficiently long period is preserved, via reproduction, in new individuals which descend from the former ones." [6] The Second Law is presented in essentially the same terms, with the added provision that both parents must have possessed the altered trait for it to be preserved in their progeny. [7] "These truths are inescapable," Lamarck concludes in corresponding passages of his compositions of 1806 and 1809. "They could only be denied by one who has never observed nature in action." [8]

In his Introduction to *Natural History of Invertebrates* (1815) Lamarck expressed an identical point of view, this time stated in the form of four laws rather than two.

In spite of the fact that Lamarck's views of evolution, based on the inheritance of changes acquired during an individual's life, were stated innumerable times, they should be reviewed here in order to characterize the methods Lamarck employed to support his convictions. This is important because such methods have been used by followers of Lamarck even in recent times.

[3] *Ibid.*, pp. 66-67.
[4] *Ibid.*, p. 111.
[5] *Ibid.*, p. 341.
[6] *Ibid.*, p. 111.
[7] *Ibid.*, pp. 341-342.
[8] *Ibid.*, pp. 111-112.

Lamarck's logical device, borrowed from ancient authors and used for many centuries before him, may be called the method of consistent instances. This consists of using as "proof" a whole list of phenomena, which depend for their explanation on a single *a priori* premise. The greater the number of similar phenomena an author manages to collect, the greater satisfaction he derives from this mental operation, and the more convincing he considers his "proof." Concerning the logical defect in such reasoning, Friedrich Engels wrote, "An accurate ordering of known phenomena of nature can itself create an impression of causality, . . . however it does not constitute proof. David Hume's skepticism is correct in its assertion that the regular repetition of *post hoc* can never establish *propter hoc.*" [9]

Lamarck never doubted that in using the method of consistent instances he was, in fact, providing proof for his laws. In chapter seven of *Zoological Philosophy,* entitled "Of the Influence of the Environment on the Activities and Habits of Animals, and the Influence of the Activities and Habits of these Living Bodies in Modifying their Organization and Structure," Lamarck specially mentioned the necessity not to content oneself by approaching such questions from general considerations. He wrote, "I am going to prove that the permanent disuse of any organ first decreases its functional capacity, and then gradually reduces the organ and causes it to disappear or even become extinct, if this disuse lasts for a very long period throughout successive generations of animals of the same race. I shall then show that the habit of using any organ, on the contrary, . . . not only perfects and increases the functions of that organ, but causes it in addition to take on a size and development which imperceptibly alter it; so that in course of time it becomes very different from the same organ in some other animal which uses it far less." [10]

To "prove" that the disuse of an organ entails its atrophy, Lamarck used such examples as: the disappearance of teeth in those animals which "acquired the habit of swallowing their food without masticating it," for example, whales, birds, anteaters; the underdevelopment of eyes in animals that lead an underground mode of life, for example, moles, mole-rats, cave salamanders; absence of legs in snakes with their highly elongated bodies—legs would hinder them in crawling through narrow crevices; and the underdevelopment of wings in certain insects that rarely fly. Lamarck also selected what he thought to be convincing examples of the consequences of an intensified use of organs. Among these he listed: the

[9] Friedrich Engels, "Dialektika prirody" ["Dialectics of Nature"], Karl Marx and Friedrich Engels, *Soch.* [*Works*], vol. XX (Moscow, 1961), p. 545.
[10] Jean Baptiste Lamarck, *Zoological Philosophy,* trans. Hugh Elliot (Fac. rpt.; New York and London: Hafner Publishing Co., 1963), p. 115.

development of webbing between digits of swimming birds, frogs, sea turtles, otter, and beaver; elongation of legs and neck in bottom-feeding wading birds; elongation of the neck only in bottom-feeding swimming birds, for example, swans and geese; elongation of the tongue in animals that feed on ant colonies (anteaters), in birds that feed on insects that live beneath tree bark, and in birds (hummingbirds) and reptiles (lizards, snakes) whose tongue serves as a sense organ or prey-capturing organ; the difference between free-swimming and bottom-dwelling fish in the location of their eyes; the development of hooves in herbivores, which must walk a great deal when grazing; the elongation of legs and neck in giraffes as the result of straining to reach leaves in trees; the development of claws in burrowing and predatory animals; the development in felines of retractible claws, which are needed to grasp prey but would hinder walking; the intense development of hind legs and tail in kangaroos, which move about by jumping; and the elongation of legs and claws in sloths, which climb slowly among trees, never leaving their tree home.

While citing these examples to illustrate or, as he thought, prove the law of the dependence of an organ's structure on the degree and character of its use, Lamarck nowhere specifically says that changes evoked by the exercise or non-exercise of organs are inheritable. Although he considered his First Law, that is, the principle of the origin of changes under the influence of function, to be verified through experience (for evidence he cited J.R. Tenon's communication describing the narrowing and foreshortening of the intestines in alcoholics), Lamarck considered his Second Law, that is, the principle of the inheritance of the results of use or disuse of organs, to be so self-evident, so indisputable, that he saw no need to cite evidence in support of it.

Though Lamarck spoke only casually about the causes of change in plants, we may conclude from his statements that he believed that the direct influence of the environment caused changes and that such changes were inheritable. Significant environmental changes "in plants where there are no activities and consequently no habits, properly socalled, great changes of environment none the less lead to great differences in the development of their parts; so that these differences cause the origin and development of some, and the shrinkage and disappearance of others. . . . . Among individuals of the same species, some of which are continually well-fed and in an environment favourable to their development, while others are in an opposite environment, there arises a difference in the state of the individuals which gradually becomes very remarkable. . . . Now if the environment remains constant, so that the condition of the ill-fed, suffering or sickly individuals becomes permanent, their internal organisation is ultimately modified, and these acquired modifications are preserved by reproduction among the individuals in question, and finally give rise to a

race quite distinct from that in which the individuals have been continuously in an environment favourable to their development." [11]

Lamarck illustrated the mutability of a plant's form under the influence of its conditions of growth with the following example: "So long as *Ranunculus aquatilis* is submerged in the water, all its leaves are finely divided into minute segments; but when the stem of this plant reaches the surface of the water, the leaves which develop in the air are large, round and simply lobed. If several feet of the same plant succeed in growing in a soil that is merely damp without any immersion, their stems are then short, and none of their leaves are broken up into minute divisions, so that we get *Ranunculus hederaceus,* which botanists regard as a separate species." [12]

Vladimir Leont'evich Komarov
(1869–1945)

Vladimir Leont'evich Komarov evaluated the logic of such arguments in a short, interesting book. "Lamarck's examples," he wrote, "do not stand up to modern criticism. . . . The water buttercup is indeed very plastic, but all this change of form is not inheritable and does not account for the

[11] *Ibid.*, p. 108.
[12] *Ibid.*, p. 111.

formation of new species. . . . Climatic and soil conditions have a tremendous influence on the form of plants; it is thought, however, that that influence is indirect, not direct. The environment does not model organisms in the way an artist molds forms from clay, rather it favors the selection of forms suited . . . to life in a given environment." [13] Regarding the famous example of the origin of the giraffe's long neck, Komarov noted, "The problem with that explanation is its simplicity. It is incomprehensible how the striving of adult giraffes to reach food high in trees could influence the mechanism of development of their offspring." [14]

In the Preface to the first volume, the editors of and commentators on the collected works of Lamarck, Ivan Mikhailovich Poliakov and Nikolai Ivanovich Kuzhdin wrote conversely with respect to Lamarck's Second Law: "Lamarck correctly . . . treats as a general biological law the principle of inheritance of traits acquired by organisms in the course of their life activity." [15] Furthermore, in his article appended to the second volume Poliakov essentially repeated the intent of his comments as he compared Lamarck's views with corresponding views that developed during the ancient period and during the sixteenth to eighteenth centuries. Poliakov acknowledged the merit of Lamarck's work with the assertion that "the inheritance of traits acquired in the course of life activity is a general rule of the evolution of organisms" [16] He wrote that he himself looked upon inheritance of acquired traits in the "broad sense" of the expression, that is, he understood it to mean all "changes in heredity" that "organisms acquire in the process of interaction with the environment." Poliakov failed to distinguish between mutations and supposedly inheritable somatic changes, and he did not discuss the heart of the matter. All this was expressed in a general, hazy discussion about "the change in typology of metabolism" (?—L.B.), about the way the evolutionary process differs on various developmental levels of the organic world, and about other topics.

Such a discussion was written in lieu of the one thing that needed to be stated and was clearly and unambiguously stated by Komarov in the passage cited above.

In a later book about Lamarck, Poliakov continued to defend the same point of view. [17] First of all, it should be noted that this book incorrectly explained the failure of Lamarck's evolutionary theory. Like the British

[13] Vladimir Leont'evich Komarov, *Lamarck* (Moscow-Leningrad, 1925), pp. 103–104.

[14] *Ibid.*, p. 114.

[15] Lamarck (n. 2), p. 848.

[16] *Ibid.*, p. 857.

[17] Ivan Mikhailovich Poliakov, *Zh. B Lamarck i ego uchenie ob evoliutsii organicheskogo mira* [*J.B. Lamarck and his doctrine on the origin of the organic world*] (Moscow, 1962), p. 266.

Lamarckian Herbert Graham Cannon, [18] Poliakov portrayed the matter too simply, by placing responsibility for the demise of Lamarck's ideas on Georges Cuvier, in particular, on the "Éloge" which Cuvier prepared for presentation to the Paris Academy of Sciences on the occasion of Lamarck's death.

Cannon accused Cuvier of a distorting presentation of Lamarck's evolutionary views, of substituting one idea for another. In Cannon's words, Lamarck spoke of changes in organs under the influence of necessity, whereas Cuvier attributed to Lamarck the assertion that animals change under the influence of their own will. Presenting Lamarck's views, Cuvier wrote, "Altered needs, altered desires in response to the surroundings, lead to altered efforts, which give rise to new organs." [19] In an excerpt from Lamarck's *Zoological Philosophy,* which Cannon cited to prove Cuvier's unfairness, these words are found: "A shore bird, which does not like to swim, and which is forced to seek food right along the shore, is constantly subject to the danger of sinking in the silt. So wanting to avoid the necessity of dipping its body in the water, the bird makes every effort to stretch and lengthen its legs." [20, 21]

In Cannon's opinion, neither Thomas H. Huxley nor Charles Darwin were familiar with Lamarck's works first hand but based their judgement of him on the opinions of Cuvier. Ignoring Darwin's statement that he had carefully read Lamarck's book, Cannon spoke as though Darwin had based his opinion of Lamarck's work solely on Cuvier's "Éloge." In Cannon's words, Darwin "never seriously studied Lamarck but based himself on that misleading idle discourse." [22]

These unfounded assertions by Cannon were repeated by Poliakov. "The 'Éloge' turned out to be a mockery of Lamarck's name and a disgraceful perversion of the original meaning of his evolutionary doctrine. In particular, Cuvier resorted to the following falsifications: Where Lamarck writes of needs and efforts, Cuvier uses the word 'desire'. . . . The 'Éloge' . . . had a pernicious influence. Many great scientists have reiterated this

[18] See the review by Leonid Iakovlevich Blacher on books by Cannon: "H.G. Cannon. *The Evolution of Living Things*. Manchester, 1958, 180 p.; Herbert Graham Cannon. *Lamarck and Modern Genetics*. Manchester, 1959, 152 p," in *Vopr. istorii estestv. i tekhn* [*questions on the History of Natural Science and Technology*], 1962, *no. 13,* 168–173.

[19] Georges Cuvier, "Eloge de M. de Lamarck," *Mém. Acad. Roy. Sci. et Inst. France* (1835), p. XIX.

[20] Lamarck (n. 2), p. 350. Lamarck used the word "to want" (voulant). In the text of "Vstupitel'nye lektsii" ["Introductory Lectures"] of 1800 and 1802, in the analogous contexts it is translated the same way: 'wanting to avoid . . ." (*op.cit.*, pp. 17 and 70). Cuvier specially noted that in presenting Lamarck's views he used the word "to want" in the sense "to have need of," i.e., in the sense Lamarck used it.

[21] [This footnote has been omitted because of redundancy; see n. 29 below.]

[22] H. G. Cannon (1959), p. 31 (see n. 18).

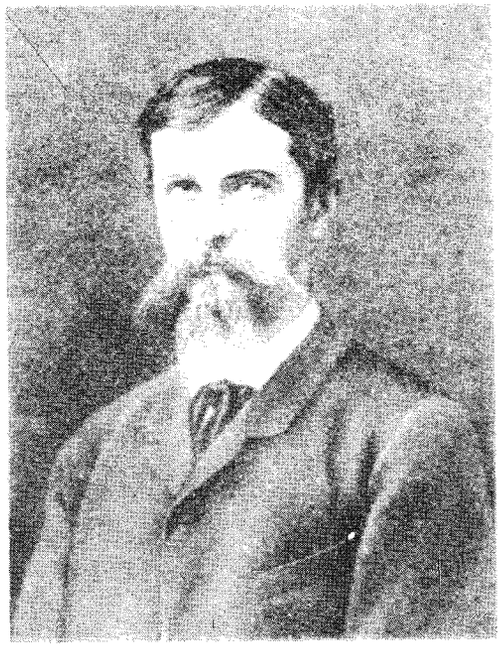
falsification instead of referring to the thorough study of the question to be found in Lamarck's original works."[23] Further, Poliakov wrote, "Darwin, Huxley, and Wallace, unfortunately, poorly understood Lamarck's work and most often simply repeated the arguments from Cuvier's 'Éloge.'"[24]

Likewise, one must regret the fact that Poliakov was himself guilty of uncritically repeating Cannon's unfounded judgement of Cuvier, Darwin, and Huxley.

In his book cited above, Poliakov went on to assert that Lamarck "had the insight to recognize the influence of the environment on the organism as a very powerful impulse toward development."[25] He gave in his Second Law a "welldeveloped formulation of the principle of inheritance of acquired characters, so important for the materialistic interpretation of living nature."[26] Poliakov credited Lamarck with the creation of "an integrated theory of the history of development in the organic world."[27] He arrived at this conclusion despite his own assertion that Lamarck did not provide a scientific, materialistic solution for the problem of organic adaptation,[28] without which there obviously cannot be an integrated, much less a materialistic, theory of evolution. In calling Lamarck a materialist, Poliakov simply ignored the fact that Lamarck equated variation in organisms with their evolution, as neo-Lamarckians of every kind have done and continue to do. Such an equation assumes that adaptation occurs under the direct influence of the environment (or through change of habits), and this further necessitates the idealistic assumption of an inherent ability to react adaptively to external influences. Poliakov also ignored these issues.

Kliment Arkad'evich Timiriazev expressed the matter very well in an article dedicated to Lamarck. "What requirements should a scientific evolutionary doctrine satisfy? It should: 1. prove the existence of an evolutionary, i.e., historical, process of transformation from certain forms into others; 2. indicate the natural factors that turn that process into progress, into improvement, in the sense of establishing a correspondence between the organism and its environment; 3. explain the apparent contradiction, fundamental to the organic world that there is a unity of the whole and yet gaps are present between the groups of all orders. The only doctrine that satisfies all three requirements is Darwinism. No other attempt before or since has satisfied all three; this applies to Lamarckism as well."[29]

[23] I.M. Poliakov (n. 17), p. 253.
[24] *Ibid.*, p. 259.
[25] *Ibid.*, p. 246.
[26] *Ibid.*, p. 232.
[27] *Ibid.*, p. 251.
[28] *Ibid.*, p. 244.
[29] Kliment Arkadievich Timiriazev, "Lamarck", *Soch.* [*Works*], vol. V (1939), p. 247. Timiriazev, "Charlz Darvin i ego uchenie" ["Charles Darwin and his Doctrine,"] in *Soch.* [*Works*], vol. VII (1939).



Kliment Arkad'evich Timiriazev
(1843–1920)

In another passage Timiriazev pointed out the distinction between "Darwin's theory and Lamarck's hypothesis that seeks in nature a simple process, the direct result of which would be an adaptive organization."[30] Further on, he said, "thinking logically, we must admit that variation evoked by the environment, is itself indifferent. . . . The stamp of adaptation is struck not by the physical process of variation but by the consistent historical process of elimination of that which is useless, i.e. by selection."[31] "Changes evoked by the environment undoubtedly exist . . . , but they don't explain why the result of this process should be adaptively structured forms. . . . The process of change proposed by Lamarck for the animal world might explain this peculiarity. . . . —necessity itself at least developed, if it did not originate, instruments for its own satisfaction. But Lamarck could not cite convincing facts to support his thesis, and the research of the last decade has shown that . . . change that is caused by exercise is not inherited. Thus, the first explanation (Lamarck's First Law), while factually true, was logically found wanting since it didn't explain

[30] K.A. Timiriazev, "Istoricheskii metod v biologii" ["Historical Method in Biology"], *Soch.* [*Works*], vol. VI (1939), p. 111.
[31] *Ibid.*, p. 163.

what needed explaining, and the second (Law), perhaps satisfactory from a general logical standpoint, was factually false.''[32]

Poliakov had also held this point of view in his earlier works. In a lecture given in May 1930 at the Fourth Congress of Zoologists, Anatomists, and Histologists in Kiev, Poliakov said that the question of the hereditary transmission of acquired traits, if by this is meant active induction of sex cells by the soma, ''has been answered in the negative, based on all genetic evidence gathered to date.'' He considered this completely natural, since one could believe in the adequate transfer of acquired traits only by proceeding from teleological principles. According to Poliakov's just conclusion, ''Lamarckism is a theory in which one sees especially graphically the formal contradiction of mechanicism and idealism, and yet one (also) sees their profound inner unity. The Lamarckism of Lamarck and that of all his followers is basically a single theory which cannot withstand criticism from the methodological or the factual standpoint.''[33]

In an article specially dedicated to criticism of the Lamarckian theory of direct adaptation, Poliakov wrote, ''(Mechanistic Lamarckians—L.B.) attribute to organisms an inherent ability to adapt themselves directly to changes in the environment. (Pike, Stavrovskii, Labbe and Hemshaw—L.B.) equate variation in organisms with evolution. Changes brought about by the inheritance of acquired traits become an integral part of the species and immediately become categories of an evolutionary order. Lamarckians do not differentiate phylogenetic and ontogenetic processes. This vulgar-mechanistic equation in their evolutionary doctrine inevitably leads Lamarckians to the acceptance of organic self-adaptation and an inherent principle of development.''[34]

If Lamarck considered the action of the environment as the basic source of changes in animals and thereby the moving force of their evolution, influencing the strengthening and weakening of organ functions and, in turn, evoking hereditary changes in organs, Etienne Geoffroy Saint-Hilaire was more a follower of Buffon in his evolutionary views. Saint-Hilaire rejected the origin of adaptations acquired by habit and proposed that the single cause of change is the direct influence of the environment even when the organisms behave completely passively in their habitat. He wrote,

[32] K.A. Timiriazev, ''Razvitie biologii v XIX v.'' [''The Development of Biology in the 19th Century''], *Soch.* [*Works*], vol. VIII (1939), p. 112.

[33] Ivan Mikhailovich Poliakov, ''Metodologiia lamarkizma'' [''The Methodology of Lamarckism''], *Tr. IV Vses. s'ezda zoologov, anatomov i gistologov* [*Annals of the Fourth Conference of Zoologists, Anatomists, and Histologists*] (Kiev-Kharkov, 1931), pp. 40–41.

[34] I. M. Poliakov, ''Pro deiaki novi riznovidnosti lamarkistskoi teorii priamogo pristosuvaniia'' [''The Methods of New Versions of the Lamarckian Theory of Direct Adaptation''], *Tr. Zoologo-biol. in-ta Khar'kovskogo gos. un-ta* [*Annals of the Zoology-Biology Institute of Kharkov State University*], 1939, *6:* 27.

Nicholai Aleksandrovich Kholodkovskii
(1858–1921)

''the environment is all-powerful in altering the form of body organization.'' Discussing the origin of gavial crocodilians from fossil teleosaurs, he asserted that atmospheric air causes ''changes in form, favorable and destructive; they are inherited and influence the entire organization of the animal. If the changes in form have harmful consequences, then the animals possessing those changes will perish and be replaced by others whose somewhat different form better suits the new environment.''[35] Saint-Hilaire gave little consideration to the mechanism of inheritance of changes brought about by the direct influence of the environment. He proposed that it is mostly the changes that arise during the embryonic stages that are passed on to progeny.

The famous Russian zoologist and historian of biology Nikolai Aleksandrovich Kholodkovskii directed special attention to the differences between views of Lamarck and Saint-Hilaire. Thus for Lamarck, the basic change-producing environmental influence was an indirect influence that acts on animals through changed needs and habits, whereas Saint-Hilaire assumed only a direct influence of environmental conditions. Kholodkovskii

[35] Etienne Geoffroy Saint-Hilaire, ''Sur le degré de l'influence du monde ambiant pour modifier les formes animales etc.,'' *Mém. Acad. Sci.*, 1833, *12:* 63–92.

thought, therefore, that "the majority of proponents of the inheritance of changes acquired during the individual's lifetime should, strictly speaking, be called Geoffroyists rather than Lamarckians, though, as a rule, they forgot the original source of their views and failed to refer to Saint-Hilaire as their predecessor."[36,37] Actually, Saint-Hilaire dealt only briefly with the question of the mechanism of the origin of changes and their fixation in progeny.

In the 1840s and 50s the Russian naturalist Karl Frantsevich Rul'e devoted much more attention to this question. A convinced proponent of the idea of the mutability of the organic world, Rul'e discussed instances of changes in animals under natural conditions as well as in the domesticated state. Like Saint-Hilaire, he saw the cause of change in the direct action of the environment. "The influence of the external world on the animal kingdom," Rul'e wrote, "is strengthened in progeny, becomes hereditary. The structure of parts of the body, the quality of functions, and the propensities of the father and mother, or whatever is acquired in an artificial mode of life, all are passed on to the offspring. . . . A short-tailed dog usually has short-tailed pups. . . . . The most trainable animals are those whose parents were trained."[38]

Rul'e's affirmation of the strict dependence of living creatures on their surrounding conditions was rather trivial even for the mid-nineteenth century, and obviously in itself in no way proved the inheritability of changes evoked by environmental influences. His confidence in the inheritance of acquired traits was not any better substantiated than the corresponding assertions of his predecessors. And the basis of his confidence —the idea of the primacy of function—was the same as that of his predecessors, Diderot, Lamarck, and others. Judging by the arguments Rul'e cited, it is clear that he did not consider it necessary to employ very exacting proof. Like Lamarck and Saint-Hilaire before him and Darwin and especially Ernst Haeckel later, Rul'e simply referred to the unverified reports of practical workers.

As already noted, Lamarck was the first to tie the question of inheritance of acquired traits directly to the problem of evolution. Rul'e also attempted to explain the evolutionary process in terms of the inheritance of acquired changes. Both of these pre-Darwin evolutionists strove for a materialistic interpretation of the historical development of the organic world. They thought that the assumption of a change-producing influence

[36] Nikolai Aleksandrovich Kholodkovskii, "Lamarkizm i zhoffruizm" ["Lamarckism and Geoffroyism"]. Article published in 1915 in the journal *Priroda* [*Nature*].

[37] *Ibid.*, rpt. in *Biologicheskie ocherki* [*Biological Sketches*] (Moscow-Petrograd: 1923), pp. 48–55.

[38] Karl Frantsevich Rul'e, "Obshchaia zoologiia" ["General Zoology"] (1850), *Izbr. biol. proizv.* [*Selected Biological Works*] (1954), pp. 127–128.

of the environment or mode of life made it unnecessary to include anything other than the material nature of the organisms themselves and of their environment in an explanation of the evolutionary process. From this point of view, the appearance of changes, especially if one assumed that these changes were responsive to external conditions, was considered the equivalent of evolution. On the other hand, the materialism of Darwin's predecessors bore all the signs of a mechanistic world view that, when carried to its logical conclusion, involved converting a theoretical view into idealism. The conception that environmental influences directly cause adaptation requires the assumption of an intelligent force that forever cares for all living creatures, that changes them in exact accordance with the changing conditions and provides for the inheritance of these changes. Another possible assumption would be that the intelligent force originally endowed living creatures with the ability to change in whatever way necessary and to pass on by heredity just what was necessary.

The last assumption is not an exaggeration. Similar views were characteristic of all followers of Lamarck, although they were not always expressed sufficiently clearly and candidly. Lamarckism that rests on idealistic premises was carried to its logical extreme in *Nomogenesis,* written by Lev Simonovich Berg. Berg's primary postulate, in contrast to the Darwinian idea of natural selection, was that "adaptation is the fundamental property of life." He wrote, "One of the corollaries of the principle of inherited adaptations, which we accept, is the doctrine of the influence of exercise and non-exercise of organs, so-called Lamarckism."[39] Reproducing the textual formulation of Lamarck's First Law and citing the example that Ludwig Plate had drawn on of the coordinated development of huge horns, thick skull, and powerful muscles of the neck and front legs in the fossil peat-bog (Irish) deer, Berg asked about the cause for such phenomena as the correlation in development of different body parts that have a stimulating influence on one another. "Why does the stimulation cause the organism to react in an adaptive manner? There is only one possible answer: this is a basic property of life. . . . If a living being possesses the ability to react adaptively to stimulation, to what avail is natural selection? Indeed, this gives the desired result immediately."[40]

An apologetic evaluation of Lamarck's erroneous and factually unfounded opinions bears nothing in common with a genuine understanding of the historical significance of his evolutionary views. Lamarck's scientific contribution lay in the fact that he replaced the prevailing view of living nature as a special act of creation, initially and forever immutable, with the

[39] Lev Simonovich Berg, *Nomogenez, ili evoliutsiia na osnove zakonomernostei* [*Nomogenesis, or Evolution Based on Natural Laws*] (Petrograd: 1922), p. 6.

[40] *Ibid.*, p. 8.

doctrine of nature's historical development, the transformation of some organic forms into other, more complex, forms. Moreover, he insightfully associated this transformation with changes in the conditions of existence.

Kholodkovskii made a definitive study of the historical significance of Lamarck's theory in a series of posthumously collected articles, *Biological Sketches.* "We must acknowledge," he wrote, "that Lamarck's basic idea—the changeability of organisms through adaptation to altered conditions—was valid. . . . This aspect of Lamarck's doctrine . . . will most likely be soon forgotten, whereas the dogma of the significance of exercise and non-exercise of organs will continue to be discredited." [41]

In its generalized form Lamarck's doctrine was a valid evolutionary theory. As the antithesis of creationism the doctrine played a positive role even in that imperfect form in which it could be revealed at the end of the eighteenth century. The postulate of the inheritance of acquired traits, which Lamarck used to defend this evolutionary conception, must be recognized as a progressive idea for its time. What other postulate could have been used at that time to argue for the possibility of the evolutionary transformation of animals and plants? What was true in the theory entered the consciousness of Lamarck's contemporaries and successors with the help of this erroneous argument. For a long time there prevailed the conviction, vividly portrayed by Herbert Spencer, that an indissoluble tie existed between the idea of evolution in the organic world and the assumption of the inheritance of acquired traits. Even Darwin could not completely free himself of this conviction, despite the fact that his brilliant idea of "the origin of species by natural selection" did not actually require such an assumption.

[41] Nikolai Aleksandrovich Kholodkovskii, "Staryi i novyi lamarkizm" ["Old and New Lamarckism"], *Sev. Vestnik* [*Northern Herald*], no. 6, 1895, rpt. in *Biologicheskie ocherki* [*Biological Sketches*] (Moscow-Petrograd: 1923), p. 30.

CHAPTER 4

Darwin's Attitude toward the Question of the Inheritance of Acquired Characters

Darwin's theory of natural selection conclusively drove idealism from biology by providing a consistently materialistic explanation for the evolution of the organic world, applicable alike to plants and animals. Yet, to the end of his life, Darwin continued to be enticed by the dominant notion of his time, that an inheritance of acquired characters was, if not a necessity, at least a real possibility. During the years when he wrote his evolutionary works, Darwin somewhat changed his views. It cannot be claimed, however, that he was developing an increasingly well-founded, consistent point of view regarding the inheritance of acquired characters. From start to finish he was troubled and unsure as to how the question should be resolved. It should be recalled that Darwin employed the same inductive reasoning method as had Lamarck and other predecessors. The time had not yet come for attempts to resolve this problem by the experimental method, the only valid method for its resolution. Darwin, however, certainly understood that the question of the inheritance of acquired characters must be decided on the basis of experiments, and he considered setting up the experiments himself. In a letter of February 6, 1881, to the German zoologist Karl Gottfried Semper, Darwin wrote, "I agree . . . that the direct action of the conditions of life on organisms, or the cause of their variability, is the most important of all subjects for the future. For some few years I have been thinking of commencing a set of experiments on plants, for they almost invariably vary when cultivated. I fancy that I see my way with the aid of continued self-fertilization. But I am too old, and have not strength enough. Nevertheless, the hope occasionally revives." [1]

In light of the absence of valid experimental data, it was quite natural that Darwin experienced doubts and vacillated in discussions of the question of whether changes acquired during the individual's life are inherited. Since practically none of his contemporaries doubted such inheritance, this vacillation is to Darwin's credit.

[1] Charles Darwin, *More Letters of Charles Darwin*, ed. Francis Darwin and A.S. Seward, 2 vols. (London: John Murray, 1903), vol. 1, pp. 391–392.

On the very first page of his "Essay of 1844," an outline of the future *Origin of Species,* Darwin wrote, "Under certain conditions, organic creatures slightly change their characteristic form, size, or other traits, even during the course of their individual lives; many of the features acquired in this manner are transmitted to progeny. . . . There is reason to believe that the strong development of certain muscles, owing to long-term exercise, as well as muscle weakening from lack of exercise, are inherited. Food and climate sometimes cause change in the color and structure of the integument of animals . . . but whether these features, acquired in such a manner during an individual lifetime, are inherited, I do not know." [2]

If Darwin found it difficult to affirm the inheritance of variations under the influence of food and climate, he doubted still more the inheritance of mechanical injury. "There are not sufficient grounds for belief in the inheritance of mutilation or variation in form caused by a mechanical influence, even if it acted over hundreds of generations." [3] Later, in his book *The Variation in Animals and Plants Under Domestication,* Darwin expressed himself differently on the same subject, without, however, supporting his change of viewpoint with new facts. "There is sufficient proof that the results of mutilation and unfortunate events . . . are sometimes inherited." [4] In 1844, Darwin admitted, though in very guarded terms, the possibility of the inheritance of results of the disuse of organs. He made the reservation that the underdevelopment of organs could also be the result of natural selection. He wrote, "There is, apparently, a certain probability that prolonged disuse of some body part or organ and the selection of individuals with these somewhat diminished parts, could create, over the course of centuries . . . races possessing those same rudimentary parts. . . . The fact that domestic ducks are less capable of flight than wild ducks must be partly due to disuse of wings over many successive generations." [5]

In the period immediately preceding publication of the *Origin of Species,* Darwin had already become convinced that species formation comes about not so much through the direct action of external conditions as through the natural selection of chance variations, and he wrote about this to friends, "external conditions (to which naturalists so often appeal) do

[2] Charles Darwin, "Ocherk 1844 g." ["Outline of 1844"], *Soch.* [*Works*], vol. 3 (Moscow-Leningrad, 1939), p. 117.

[3] *Ibid.*, p. 119. Francis Darwin commented on this passage, "It is interesting to note that although Darwin, like his contemporaries, believed in the inheritance of acquired traits, he excluded instances of mutilation" (p. 774).

[4] Charles Darwin, *Izmeneniia domashnikh zhivotnykh i kul'turnykh rastenii*" [*Variation in Animals and Plants Under Domestication*], *Soch.* [*Works*], vol. IV (Moscow-Leningrad, 1951), p. 500. [*Variation in Animals and Plants Under Domestication,* 2 vols. (2nd ed., New York: D. Appleton, 1897). Corresponding English passage could not be located].

[5] Darwin (see n. 2), pp. 218-219.

by themselves *very little.*" [6] "I most entirely agree with you on the little effects of 'climatal conditions,' which one sees referred to *ad nauseum* in all books." [7]

In the Introduction to the *Origin of Species,* Darwin pointed out the inevitability of the conclusion that species undergo modification, acquiring "that perfection of structure and coadaptation which most justly excites our admiration." He continued, "Naturalists continually refer to external conditions, such as climate, food, etc., as the only possible cause of variation . . . but it is preposterous to attribute to mere external conditions, the structure, for instance, of the woodpecker . . . and . . . of the mistletoe." [8]

In reference to this passage, Kliment Arkad'evich Timiriazev wrote, "Therefore, in the very first lines of his book, Darwin properly regards the influence of the environment. He does not hesitate to label as 'preposterous' the attempts to explain the adaptive structure of organisms by this factor alone." [9]

General considerations regarding the manner of the origin of variations under the action of the conditions of life were presented in chapter one of the *Origin of Species.* Darwin assumed that external agents may act in two ways: directly, on the whole organization of the living creature or on its individual parts; and indirectly, through the reproductive system. With respect to the direct action of the environment, in the last edition of the *Origin* published during his lifetime, Darwin specially stated, referring to Weismann's opinion as well as his own as presented in *Variation under Domestication,* that variations correspond not to the nature of the conditions, but to the nature of the organism itself. Thus he felt that "nearly similar variations sometimes arise under, as far as we can judge, dissimilar conditions, and, on the other hand, dissimilar variations arise under conditions which appear to be nearly uniform." [10] In a section of the same chapter, entitled "Effects of Habit and of the Use or Disuse of Parts," Darwin repeated his proposal that domestic ducks have underdeveloped wings as the result of disuse. Having shown the difference between domestic and wild ducks with respect to the weight of their wings and leg bones, he now without reservation attributed this difference to function,

[6] Charles Darwin, "Letter to Hooker, November 23, 1856," *Life and Letters of Charles Darwin,* ed. Francis Darwin 2 vols. (New York: D. Appleton & Co., 1897), 1, 445.

[7] Darwin, "Letter to Wallace, May 1, 1857," *ibid.*, p. 453.

[8] Charles Darwin, *Proiskhozhdenie vidov* [*Origin of Species*], *Soch.* [*Works*], vol. 3, p. 271. [(Facs. of 1st ed.; Cambridge, Mass: Harvard Univ. Press, 1963), p. 3.]

[9] Kliment Arkadievich Timiriazev, "Faktory organicheskoi evoliutsii" ["Factors in Organic Evolution"]. Speech given at the third general meeting of the VIII Congress of Russian Natural Historians and Doctors (1890). In Darwin, *Soch.* [*Works*] (1938), vol. 5, p. 129.

[10] Darwin (n. 8), p. 275. [Passage does not appear in the first edition but see 6th ed.; New York; Appleton & Co., 1897; vol. 1, p. 8.]

that is, to the reduced use of wings and the increased use of legs among domestic ducks. He proposed that the development of cows' and goats' udders is due to the exercise they receive through milking. He also noted the probability that the trait of drooping ears in domestic animals arose because of a lack of exercise of the muscles of the ear pinna, since domestic animals have less occasion than wild animals to cock their ears to avoid danger.

In *Variation under Domestication,* Darwin spoke once again, though more cautiously, about the origin of drooping ears in domestic animals. "The incapacity to erect the ears is certainly in some manner the result of domestication; and this incapacity has been attributed by various authors to disuse." In a footnote to this passage, Darwin cited the opinion of Martin Wilckens, who "argues strongly against the belief that the drooping of ears is the result of disuse."[11] Following this, Darwin considered one more example, which he spoke of with an obvious hint of irony addressed to those who too eagerly attributed change in the structure of animals to the use and disuse of organs: "The tail of no wild animal, as remarked to me by Mr. Blyth, is curled; whereas pigs and some races of dogs have their tails much curled. This deformity, therefore, appears to be the result of domestication, but whether in any way connected with the lessened use of the tail is doubtful."[12]

Darwin returned to similar examples in chapter five of the *Origin of Species* ("The Laws of Variability"). In one section he listed several instances of variation which, in his opinion, were explainable in terms of the use and disuse of organs. He expressed his opinion on this theme in a rather categorical assertion. "I think there can be no doubt that use in our domestic animals has strengthened and enlarged certain parts, and disuse diminished them; and that such modifications are inherited." With respect to wild animals, Darwin was forced to express himself more carefully. "Under free nature, we have no standard of comparison, by which to judge of the effects of long-continued use or disuse . . . but many animals possess structures which can be best explained by the effects of disuse."[13]

In chapter seven of the *Origin of Species,* entitled "Miscellaneous Objections to the Theory of Natural Selection," Darwin again addressed the question of the inheritance of variation caused by the activity of an organ; in particular he addressed himself to the cause for the asymmetric placement of eyes in flounder. George Mivart had objected that a gradual displacement of the eye from the side of the head facing bottom to the opposite side could not be explained by the principle of natural selection since there could be no advantage to a slight displacement

[11] Darwin (n. 4), p. 680. [English edition: vol. 2, p. 291.]

[12] *Ibid.*, p. 681 [p. 291.]

[13] Darwin (see n. 8), p. 369. [Ist ed., p. 135; 6th ed., vol. 1, p. 167.]

of the eye. In this case Darwin was willing to admit that "the first stages of the transit of the eye from one side of the head to the other . . . may be attributed to the habit . . . of endeavouring to look upwards with both eyes."[14] Furthermore he felt that the pressure involved in twisting the lower eye upwards must have led to an inheritable deformation of the skull, that is, to a displacement of the orbit. Thomas Hunt Morgan cited this discussion in particular as an example of Darwin's inconsistency, of his failure to see a contradiction between natural selection and Lamarckian ideas of the inheritance of results of use and disuse, and of his choice of a middle course which embraced both theories.[15]

Darwin changed his views in later editions of the *Origin of Species,* undoubtedly under the influence of his contemporary naturalists who could not, of course, provide genuine proof of the inheritance of functional or other acquired changes, but merely added to the number of examples in which such inheritance was assumed *a priori.* In the sixth edition, the following passage appears: "Species have changed in a long course of development. This was achieved mainly by means of the natural selection of countless consecutive minute favorable variations [facilitated, in an essential way, by the inherited effects of the use and disuse of organs; a less essential role in creating adaptive structures, past and present, was played by the direct action of external conditions.]"[16]

In print and in his correspondence Darwin focused his discussion of the basic principles of evolution, as formulated in the *Origin of Species,* mainly on the very existence of natural selection in nature and its significance for the processes of species formation. Darwin's critics and correspondents considered the antithesis of natural selection to be direct adaptation, that is, the inheritance of adaptive changes that arise in the course of an individual's lifetime.

Darwin's inherent, scrupulous scientific conscientiousness and humility caused him to listen carefully and patiently to all judgements of his views. His letters of the period 1859–1868, that is, from the release of the first edition of the *Origin of Species* to the publication of *Variation under Domestication,* clearly reflect his apprehension that he may have exaggerated the role of natural selection in the evolution of the organic world. First of all, Darwin repudiated charges that he thought of natural selection as the cause of variation. In a letter to the botanist William Harvey (August 1860), he pointed out that he had never spoken of natural selection as the "sole agency of modification": "I have over and over again, *ad nauseam,*

[14] *Ibid.*, p. 443. [6th ed., vol. 1, pp. 292–293.]

[15] Thomas Hunt Morgan, *Evolution and Adaptation* (New York: Macmillan and Co., 1903). Quotation from an article by Garland E. Allen, "Thomas Hunt Morgan and the Problem of Natural Selection," *J. History of Biology*, 1968, *1:* 113–139.

[16] Darwin (see n. 8), p. 659. In brackets are the words absent from the first edition of *Origin of Species.* [Passage taken from Russian text.]

directly said . . . that selection can do nothing without previous variability. . . . I consider Natural Selection as of such high importance, because it accumulates successive variations in any profitable direction, and thus adapts each new being to its complex conditions of life." [17] In the period following publication of the *Origins* Darwin continued to emphasize that adaptation is a consequence of selection, not of responsive variations. He was undoubtedly troubled by charges that he underestimated the evolutionary significance of conditions of life. He spoke of this several times, in particular, in a letter dated October 4, 1867 to Charles Lyell. [18]

On March 18, 1862 in a letter to Joseph D. Hooker, Darwin drew attention to the fact that the degree of variability always depends on the degree of disturbance of that species' usual conditions of life. "There is more variability and more monstrosities . . . under unnatural domestic conditions than under nature." [19] This letter also showed that Darwin attributed the influence of changed conditions to their effect on the reproductive organs, that is, he considered the source of new forms to be that which August Weismann later termed "blastogenic changes." In another letter to Hooker (November 20, 1862) Darwin returned to the question of the source of adaptation. "My enormous difficulty for years was to understand adaptation, and this made me, I cannot but think, rightly, insist so much on Natural Selection." [20]

Two letters to Hooker, separated by only a two-week interval, serve as evidence of Darwin's vacillation in resolving the dilemma of natural selection and direct adaptation. In the first of these (November 24, 1862), Darwin wrote, "My present work (preparation of *Variation under Domestication*) is leading me to believe rather more in the direct action of physical conditions. I presume I regret it, because it lessens the glory of Natural Selection, and is so confoundedly doubtful." [21] But on December 12 of the same year, Darwin expressed essentially the opposite opinion: "Plants being identical under very different conditions has always seemed to me a very heavy argument against what I call direct action." [22] Two months later, on February 16, 1863, answering a letter to Dr. Horace Benge Dobell, author of *On the Germs and Vestiges of Disease* (1861), Darwin again revealed how much anxiety this problem caused him. He wrote, "I can see that the conditions of life must play a most important part. . . . How far these conditions act on 'the forms of organic life' I do not see clearly." [23]

[17] Darwin (n. 1), vol. 1, pp. 160–161.
[18] *Ibid.*, pp. 299–300.
[19] *Ibid.*, p. 198.
[20] *Ibid.*, p. 213.
[21] *Ibid.*, p. 214.
[22] *Ibid.*, p. 222.
[23] *Ibid.*, p. 235.

In *Variation under Domestication* Darwin cited many examples for which he proposed, in the absence of exacting proof, that the development and the disappearance of organs were due respectively to an intensified and diminished function. The origin of many other organs, however, could not in his judgement be explained by intensified use. In a letter to George Henry Lewes, dated August 7, 1868, Darwin wrote, "If you mean that in distinct animals, parts or organs, such for instance as the luminous organs of insects or the electric organs of fishes, are wholly the result of the external and internal conditions to which the organs have been subjected, in so direct and inevitable a manner that they could be developed whether of use or not to their possessor, I cannot admit (your view). . . . Such organs as those above specified seem to me much too complex and generally too well co-ordinated with the whole organisation, for the admission that they result from conditions independently of Natural Selection. . . . From their perfect coadaptation (of claws and hooves) with the whole rest of the organisation, I cannot admit that they would have been formed by the direct action of the conditions of life." [24]

The question of the correlation between, on the one hand, the direct influence of the environment, habits, and function of various intensities, in short, the inheritance of acquired characters and, on the other hand, the indirect influence of the environment, the action of natural selection, was given a very thorough examination in *Variation under Domestication.* It is instructive to consider specially those instances in which Darwin could not decide whether he was dealing with an inherent or an acquired trait. He regarded drooping eyelids (ptosis) as an example of an individual variation that becomes hereditary, on the basis of a case in which a father, who had acquired ptosis as a child, transmitted that trait to two of his three children. In Darwin's opinion, nearsightedness was not an inherent trait. "This condition is not commonly congenital, but comes on in youth, the liability to it being well known to be transmissible from parent to child. . . . There is ground for believing that it may often originate in causes acting on the individual affected and may thenceforth become transmissible." [25]

Darwin's doubts were especially obvious when he vacillated between the assumption of the inheritance of the results of exercise and the possibility of explaining the same phenomena by the activity of natural selection. "When we learn that long before the birth of infants the skin on their palms and soles is thicker than on any other part of the body, . . . we naturally are inclined to attribute this phenomenon to the inheritance of the results of prolonged use or pressure. It is tempting to extend that view even to the hooves of mammals; but who will pretend to decide to what

[24] *Ibid.*, pp. 306–307.
[25] Darwin (n. 4), p. 443 [English edition: vol. 1, p. 453.]

extent natural selection can facilitate the formation of a structure so obviously important for the animal?" [26] Referring to reports that under experimental conditions the degree of development of gills and lungs in *Proteus* depends on the water level, Darwin commented, "Such variations hold little interest for us since we don't know whether they have a tendency to be inherited." [27]

Darwin gave special consideration to the inheritance of variations caused by the direct action of the environment, particularly in plants. In the twenty-third chapter of *Variation under Domestication,* he included with characteristic objectivity a number of "facts . . . that suggest that climate, food, and other factors had such a definite and powerful influence on organization, . . . that thanks to them, and without the assistance of selection, new subspecies or races were formed," and he balanced these with "facts and opinions that contradict such a conclusion." Darwin intended to weigh, "as impartially as possible, the evidence in favor of each viewpoint." [28]

Naturally, the facts and opinions belonging to the second viewpoint have the greatest interest, since they represent the independent thinking of Darwin, his attempt to free himself from the generally accepted views.

Darwin wrote, "There are a great number of variations which can scarcely be attributed to the definite action of external conditions, thus the alteration of the skull in Niata cattle and the bulldog, long horns in Kafir cattle, fused digits in fused-toed swine, the huge feather crest and inflated skull in Polish hens, and the throat pouch in grouse. In all cases, there must exist some causative factor. Since we see countless numbers of individuals living under approximately identical conditions and since the variation happens in only one of them, we may, however, conclude that the constitution of the individual has much greater significance than the conditions in which it is found." [29] Further on he wrote, "The degree of change which occurred in animals and plants under domestication does not correspond to the degree of change in conditions they were subjected to. . . . The dove changed in Europe probably more than any other bird; yet it is an indigenous species and was not subjected to the influence of any unusual changes in conditions." [30]

In summary, Darwin noted that "it is extremely difficult to distinguish between the definite result of changed conditions and the accumulation

[26] *Ibid.*, p. 677 [Corresponding English passages could not be located for footnotes 26–32.] Darwin wrote elsewhere about thickening of skin on the soles and palms of the human foetus as evidence of the inheritance of the results of pressure, *Descent of Man, Soch.* [*Works*], vol. 5 (1935), p. 160.

[27] Darwin (see n. 4), p. 678.

[28] *Ibid.*, p. 657.

[29] *Ibid.*, p. 668.

[30] *Ibid.*, pp. 669–670.

through natural selection of indefinite variations that proved valuable," [31] and that "We are coming to the firm belief that . . . the nature of a variation depends only to a small extent on the conditions in which a plant grows, and is much more dependent upon the hereditary nature or constitution of the whole group of related plants to which the given plant belongs." [32]

Reviewers of Darwin's works sometimes attributed to him a firm belief in the inheritance of acquired traits. A case in point is the article by Nikolai Ivanovich Nuzhdin that introduces the fourth volume (containing *Variation under Domestication*) of the nine-volume Russian collection of Darwin's works. We should point out that this collection includes extensive commentaries and is the most complete of any of the collected works of Darwin in the world. Its publication lends undeniable credit to its Soviet researchers, especially to the editors-in-chief V.L. Komarov, V.N. Sukachev, and S.L. Sobol'. Since this collection will long be used in the study of Darwin's scientific legacy, it is important to give due consideration to Nuzhdin's accompanying article. In Nuzhdin's words, "Darwin expresses an incorrect view in questioning the direct relation between variations and the conditions of life." [33] In another passage Nuzhdin reproached Darwin for "underestimating the role of the direct action of conditions of life on the organism and misunderstanding the adaptive character of the resulting variation, and for overestimating the role of selection in evolution." [34] As "proof" that Darwin attached great significance to predetermined variations, Nuzhdin cited excerpts in which Darwin, in fact, expressed himself most carefully, using such expressions as "apparently" (pp. 126, 137), "could not a difference in climate . . . have caused?" (p. 167), and "perhaps" (p. 171). Nuzhdin wrote: "Darwin did not doubt that organs vary under the influence of use and disuse, and that such variations are transmitted by heredity." [35] From these statements quoted above it can indeed be inferred that Darwin had little doubt of the possibility of inheritance of such variations. However, Nuzhdin himself, in support of his assertions, refers to a letter from Darwin to Hooker, in which Darwin wrote, "I think that 'use and disuse' have, at least, a certain influence." Nevertheless, Nuzhdin repeated his assertion that Darwin was, "without a doubt, an advocate of the inheritance of acquired characters." [36]

N.I. Feiginson likewise incorrectly asserted that "C. Darwin accepted,

[31] *Ibid.*, p. 672.

[32] *Ibid.*, p. 673.

[33] Nikolai Ivanovich Nuzhdin, "Znachenie raboty Ch. Darvina 'Izmeneniia domashnikh zhivotnykh i kul'turnykh rastenii" ["The Significance of C. Darwin's 'Variation in Animals and Plants Under Domestication'"], in Charles Darwin, *Soch.* [*Works*], vol. 4 (1951), p. 27.

[34] *Ibid.*, p. 37.

[35] *Ibid.*, p. 40.

[36] *Ibid.*, p. 60.

without reservation, the principle of inheritance of acquired characters.'' [37] He referred to those passages from the *Origin of Species* where Darwin had written that the enlargement of udders in milk cows and goats ''represents, *probably,* an example of exercise,'' and that drooping ears in domestic animals were *probably* the result of disuse [Editors' emphasis]. Besides these, Feiginson mentions seven chapters from *Variation under Domestication,* in only two of which does Darwin write of the possible direct influence of environment and organ function. The quotations from these chapters were cited earlier and they do not support the assertions of Nuzhdin and Feiginson.

To argue for the inheritance of acquired characters, Nuzhdin even made use of Darwin's obviously mistaken notions, for instance, the idea of ''the influence of the male element on subsequent offspring of the female mated with a second male.'' [38] This is the concept of telegony, a belief which represented one of the curious prejudices that was widespread in animal husbandry before the beginning of the twentieth century. The most popular source of this prejudice, and one familiar to Darwin, was the report that an Arabian mare, having previously borne a foal by a quagga, subsequently bore a foal by an Arabian stallion, and the latter foal had certain traits reminiscent of the quagga. [39] Until that report was carefully investigated by James Cossar Ewart, people believed in telegony and took that invalid report as evidence that the spermatozoa of the first male acts upon the soma of the female to alter it and that the altered soma of the female acts upon her ova.

Reviews have already been published of the incorrect evaluations of Darwin's views that are found in course textbooks on Darwinism. [40, 41] Here it is necessary to mention only the issues that shed light on Darwin's ideas of the source and direction of hereditary variability. It was Darwin's opinion that ''indefinite variability is a much more common result of changed conditions than definite variability, and has probably played a more important part in the formation of our domestic races.'' [42] Darwin repeated this thought many times as a basis for the principle of selection in nature. Despite this, one textbook author stated that ''it is precisely this [definite] variability which Darwin considers the most significant in evolution'' (Dvoriankin, p. 139). Another author unjustifiably asserted that ''as the basis of his doctrine on transformation of organs, Darwin posited Lamarck's principle of the phylogenetic significance of use and disuse of organs'' (Lebedev, p. 226). In other passages we find statements such as: ''Darwin definitely spoke in favor of the inheritance of acquired traits'' (Lebedev, p. 117) and ''for Darwin, the inheritability of divergences acquired by the individual . . . was not in doubt'' (Dvoriankin, p. 143).

[37] N.I. Feiginson, *Korpuskuliarnaia genetika. Kriticheskii obzor* [*Corpuscular Genetics: A Critical Review*] (Moscow, 1963), p. 328.

[38] Darwin (n. 4), p. 424 [Corresponding English passage could not be located.]

[39] There is a more detailed discussion of telegony in chapter 7.

[40] Abram L'vovich Zelikman, a review article on textbooks by N.V. Lebedev (1962) and by Fedor Andreevich Dvoriankin (1964) in *Genetika* [*Genetics*], 1965, *No. 2:* 170–175.

[41] Kirill Mikhailovich Zavadskii and Zelman Isaakovich Berman, an article in *Vestnik Leningr. Un-ta* [*Leningrad Univ. Herald*], 1966, *no. 9:* 5–22.

[42] Darwin (n. 8), p. 275. [Corresponding English passage could not be located].

It was rather widely believed that Darwin radically altered his stance on the evolutionary significance of direct adaptation. But analysis of Darwin's published works, the changes he made in the text of later editions, and letters he wrote in various years allow us to see the incorrectness of such a view. In his article, Nuzhdin very clearly demonstrated this point of view; he supported it by contrasting Darwin's letters to Joseph Hooker (1862) and Moritz Wagner (1876). In the letter to Hooker (March 18, 1862), Darwin wrote, ''I have for years and years been fighting with myself not to attribute too much to Natural Selection . . . perhaps I have too much conquered my tendency to lay hardly any stress on conditions of life.'' [43] Darwin expressed himself in the letter to Wagner (October 13, 1876) with still greater certainty, ''In my opinion the greatest error which I have committed, has been not allowing sufficient weight to the direct action of the environment, i.e., food, climate, etc., independently of natural selection.'' [44]

In referring to these excerpts, Nuzhdin wrote, ''This is not a casual admission, written under some temporary impression, but a firm belief in . . . the immense role of the conditions of life. . . . From then on Darwin did not change his mind on this point.'' [45]

In reality, during the years afterward, Darwin several times expressed his previous doubts concerning the relative contributions of direct adaptation and natural selection as the active force of species formation, emphasizing the significance now of one, now of the other.

In 1880, in the introduction to *Voyage of the Challenger,* Charles Wyville Thomson commented that ''the character of abyssal fauna refuses to give the least support to the theory which refers the evolution of species to extreme variation guided only by natural selection.'' In a letter to the editor of *Nature,* dated November 11, 1880, Darwin expressed the regret that ''Sir Wyville Thomson does not understand the principle of natural selection; otherwise he could not have written [such a] phrase.'' ''Can Sir Wyville Thomson name any one who has said that the evolution of species depends only on natural selection? As far as concerns myself, I believe that no one has brought forward so many observations on the effects of the use

[43] Darwin (n. 1), vol. 1, p. 198.

[44] Darwin (n. 6), vol. 3, p. 159. [Passage follows the English vol. 2, p. 338.]

[45] Nuzhdin (n. 33), p. 24.

and disuse of [various] parts [of the body], as I have done in my *Variation of Animals and Plants under Domestication*. I have likewise there adduced a considerable body of facts showing the direct action of external conditions on organisms." [46]

This remark, published in a popular natural history journal, was obviously intended to eliminate grounds for the often repeated accusation that Darwin continued to insist on a monopolizing role for natural selection. It is a rare instance of his engaging in polemics in print, but in general, as Darwin wrote in his *Autobiography,* he followed Lyell's advice "never to get entangled in a controversy as it rarely did any good and caused a miserable loss of time and temper." [47]

Still, it would be a mistake to think that at that time Darwin had come to a definite conclusion about how significant a role direct adaptation plays compared to the role of natural selection. The content of a letter addressed to the Würzburg zoologist Karl Semper, dated July 19, 1881, is very significant in this respect: "I thought that you attributed too much weight to the *direct* action of the environment." Further on in the letter Darwin referred to the review in which Professor Hermann Hoffmann summarized his own articles concerning variation in plants in the *Botanische Zeitung,* "it is really surprising how little effect he produced by cultivating certain plants under unnatural conditions, as the presence of salt, lime, zinc, etc., etc., during *several* generations. . . . No doubt I originally attributed too little weight to the direct action of conditions, but Hoffmann's paper has staggered me. . . . Hoffmann even doubts whether plants vary more under cultivation than in their native home and under their natural conditions. If so, the astonishing variations of almost all cultivated plants must be due to selection and breeding from the varying individuals. This idea crossed my mind many years ago, but I was afraid to publish it, as I thought that people would say, 'how he does exaggerate the importance of selection.' I still *must* believe that changed conditions give the impulse to variability, but that they act *in most cases* in a very indirect manner." [48]

Sergei S. Chetverikov saw the cause of Darwin's increased tendency to limit the significance of natural selection in favor of Lamarckian factors in the following circumstance. [As he pointed out] the engineer Fleeming Jenkin used in 1867 a simple calculation to show that, under conditions

[46] Charles Darwin, "Ser Uaivil Tomson i estestvennyi otbor" ["Sir Wyville Thomson and Natural Selection"], *Soch,* [*Works*], vol. 3 (1939), p. 754 [Passage follows original: *Nature,* 1880, *23:* 32.]

[47] Charles Darwin, *Vospominaniia o rasvitii moego uma i kharaktera* [*Reminiscences of the Development of My Mind and Character*], trans. S.L. Sobol' (Moscow, 1957), p. 136 [See *The Autobiography of Charles Darwin, 1809–1882,* ed., Nora Barlow (New York: W.W. Norton & Co., 1969), p. 126.]

[48] Darwin (n. 6), vol. 3, pp. 344–345. [Passage follows the English: vol. 2, pp. 516–517.]

of free interbreeding, any chance deviation that arises, even if it is useful, will be quickly lost among the multitude of unaltered individuals. Referring to Jenkin, Darwin said that interbreeding acts to swamp each newly arising individual deviation, even rather abrupt deviations. These objections to Darwin's emphasis on individual deviations as the raw material of natural selection (this "Jenkin's nightmare" disturbed Darwin as long as he lived) "deflected the theoretical thought of Darwin from his *earlier* and *more accurate* concepts in the direction of acceptance of views closer to current neo-Lamarckism." [49]

In their desire to prove that Darwin increasingly favored Lamarckian factors in evolution, commentators claimed that Darwin even changed his attitude toward Lamarck's theory as a whole. In this vein, Nuzhdin cited three references Darwin made to Lamarck's book. In the first two (to J.D. Hooker in 1844) and the third (to Asa Gray in 1857 [1860?]), Darwin called the book veritable rubbish and said that it is futile to explain adaptation to the biotic environment by means of the action of climate or Lamarckian habit. [50] Nuzhdin commented, "The evaluation of Lamarck which Darwin gave later in his "Historical Sketch," a preface to the third edition of the *Origin of Species,* sounds completely different." [51] In this sketch, Darwin credited Lamarck for upholding the "doctrine that all species, including man, are descended from other species," and for arousing attention to the "probability of all change in the organic, as well as in the inorganic world, being the result of law, and not of miraculous interposition." [52] He made no mention of Lamarck's views on the causes of evolution, clearly to avoid, in print, speaking ill of his predecessor. We may now turn to the third of Darwin's references to Lamarck's book, as cited by Nuzhdin. Lyell had compared the works of Darwin and Lamarck. In a letter, Darwin pointed out the inappropriateness of a comparison between his work and Lamarck's book, which "I consider, after two deliberate readings, as a wretched book." [53] This letter is dated March 12, 1863, that is, it was written two years after the "Historical Sketch" in the third edition of the *Origin of Species*

[49] Sergei Sergeevich Chetverikov, "O nekotorykh momentakh evoliutsionnogo protsessa s tochki zreniia sovremennoi genetiki" ["On Certain Aspects of the Evolutionary Process From the Standpoint of Modern Genetics"], *Zhurn. Eksp. Biol.* [*Journal of Experimental Biology*], 1926, ser. A, 2. Reprinted in *Biull. Mosk. ob-va ispyt. prir., otd. bil.* [*Bulletin of the Moscow Society of Experimenters in Nature, Biological Division*], 1965, *70:* 44. [Passage quoted follows translation done by Malina Barker (ed. I. Michael Lerner) *Proc. Am. Phil. Soc.,* 1961, *105:* 175.]

[50] Darwin (n. 6), vol. II, pp. 29 and 121. [For Hooker passage see vol. 1, pp. 41 and 43; for Gray passage see vol. 1, p. 153.]

[51] N.I. Nuzhdin (n. 33), p. 45.

[52] Darwin (n. 8), pp. 261–262. [The "Historical Sketch" appeared in the 3rd through 6th editions.]

[53] Darwin (n. 6), vol. III, p. 14 [Passage follows the English original: vol. 2, p. 199.]

published in April 1861. Therefore, Nuzhdin's claim that Darwin changed his attitude toward the principles of Lamarck is unfounded.

There is no doubt that Darwin seriously pondered the consequences of assuming the possibility of inheritance of acquired changes.

After enumerating examples which might be assigned to the category of inheritance of acquired characters, Darwin posed the following question: "How, again, can we explain the inherited effects of the use or disuse of organs? . . . How can the use or disuse of a particular limb or of the brain affect the small aggregate of reproductive cells, seated in a distant part of the body, in such a manner that the being developed from these cells inherits the characters of either one or both parents?" [54]

There are really only two answers to that question: either we must admit that such a long-distance influence of somatic cells on sex cells, acting adequately to change the sex cells, is impossible; or, having assumed the possibility of such an influence, we must devise a hypothetical explanation for the mechanism of the influence. Darwin did not choose the first, the negative, answer; belief in the inheritance of acquired changes was too widely accepted. There remained the second path, and Darwin set out on it by proposing a "provisional hypothesis of pangenesis."

Darwin constructed this hypothesis on the same premises that Hippocrates had posed 2300 years earlier and against which Aristotle had convincingly argued. Among his predecessors, Darwin cited, with certain reservations, Ray, Buffon, Bonnet, Spencer, and Mantegazza. His concepts were also close to the views of Erasmus Darwin and Maupertuis. [55]

Darwin's hypothesis of pangenesis rests on a concept of submicroscopic gemmules, capable of being transported by the circulatory system to the sex cells. The gemmules, given off by somatic parts of the organism, gather in the sex elements and transmit to them the changes that arose in various parts of the body, so that the offspring which develop from these sex cells receive the corresponding changed traits. Though he developed his hypothesis in quite some detail and cited facts which, in his opinion, could support it, Darwin nevertheless looked upon the hypothesis of pangenesis as a provisional solution to the problem, and he was not satisfied with it.

Between publication of the first and second editions of *Variation under Domestication,* which contained Darwin's hypothesis of pangenesis, many authors spoke out on the subject. In the second edition, Darwin mentioned critical comments by Delpino, St. George Mivart, Wigand, and others, and he gave special attention to objections made by Francis Galton, the only

[54] Darwin (n. 4), p. 736 [Passage follows the English: vol. 2, p. 367.]

[55] See chapter 2 of this work.

critic who answered the hypothesis not with verbal reasoning but by conducting an appropriate experiment. [56]

Francis Galton
(1822–1911)

Galton later wrote about his experiment, "That the gemmules are not contained, in any large number, in the bloodvessels, is proved by my own experiments, in which I largely transfused the blood of an alien species of rabbit into the blood-vessels of male and female silver-grey rabbits, from which I afterwards bred. I repeated this process for three generations, and found not the slightest sign of any deterioration in the purity of the silver-grey breed." [57] Galton noted that transferral of gemmules from the tissues to the sex glands is *a priori* quite improbable, since gemmules, possessing a colloid nature, could not freely pass through membranes. Galton transfused blood from one variety of rabbit to another and, as Darwin wrote,

[56] Francis Galton, "Experiments in Pangenesis by Breeding from Rabbits of a Pure Variety, into Whose Circulation Blood Taken from Other Varieties had been Largely Transfused," *Proc. Roy. Soc. London,* 1871, *19:* 394–410.

[57] Francis Galton, "A Theory of Heredity," *J. Anthropol. Inst. Gr. Britain and Ireland,* 1875. *5:* 341–342.

"among the very numerous offspring there was no sign of hybridism." "I certainly should have expected," Darwin continued, "that gemmules would have been present in the blood, but this is no necessary part of the hypothesis, which manifestly applies to plants and lowest animals."[58] This provision rendered the hypothesis inapplicable to the majority of animals, namely, all those which possess circulatory systems of blood and lymph.

Four years after the publication of his pangenesis hypothesis, Darwin wrote to Ernst Haeckel (December 27, 1871), "My ideas have been almost universally despised, and I suppose that I was foolish to publish them; yet I must still think that there is some truth in them."[59]

Several years earlier, however, when Darwin was still preparing *Variation under Domestication* for publication, he already doubted the validity and fruitfulness of the pangenesis hypothesis and, as Timiriazev wrote, "He himself gave it this severe condemnation: 'It is all rubbish to have speculated as I have done.'"[60]

That Darwin still occasionally reflected on this hypothesis, which he much later, in a letter to George John Romanes, called "an airy nothing,"[61] is evidenced only in correspondence, not in printed works. Darwin wrote the letter to Romanes while still reacting to an essay by Haeckel. He said that Haeckel was merely "attacking Pan-[genesis] and substituting a [his own] molecular hypothesis."[62] Darwin was very doubtful that, in accordance with Haeckel's hypothesis, oscillation in the "formative protoplasm" could explain exercise-dependent changes in organs and the inheritance of such changes. To Darwin it was still less comprehensible how Haeckel's hypothesis could be applied "in cases like those of Lord Morton's mare." In this case, as Darwin put it, Haeckel would say, "that the vibrations from the protoplasm, or 'plasson,' of the seminal fluid of the zebra set plasson vibrating in the mare and that these vibrations continued until the hair of the second colt was formed, and which consequently became barred like that of a zebra."[63] In a letter to Ernst Ludwig Krause, in which he discussed the puzzling phenomenon of regeneration of a crab's claw that resulted in an appendage reminiscent of the limb of an ancestral form,

[58] Darwin (n. 4), p. 724 n. [Passage follows the English: vol. 2, p. 350 n.]

[59] Darwin (n. 1), vol. 1, p. 335.

[60] Kliment Arkad'evich Timiriazev quoted Darwin in "God itogov i pominok" ["Year of Summaries and Memorials"], *Soch.* [*Works*], vol. IX (1939), p. 102. Darwin's words are from his letter to Thomas H. Huxley, presumably written 1865. [Passage follows the Russian (n. 6), vol. 3, p. 45.]

[61] Darwin, "Letter to G.J. Romanes, 29 May 1876," (n. 1) [vol. 1, pp. 363–364.]

[62] For Haeckel's views on inheritance, see chapter 5.

[63] Darwin, "Letter to G.J. Romanes, 29 May 1876," (n. 1) [passage follows English original: vol. 1, p. 364.]

Darwin gave his opinion that "this instance argues in favor of the pangenesis hypothesis, which scarcely has a friend in this world."[64]

To unify his whole theory, Darwin felt the need for a single conception that would encompass the phenomena of individual development, variability, heredity, and phylogenetic development. He proposed pangenesis as that single, unifying conception, but he failed to offer precise empirical data. Such data would have rendered the hypothesis scientifically groundless.

The above discussion of the hypothesis of pangenesis should serve as material for present-day commentaries on the subject.

In his third book dedicated to the problems of evolution, *The Descent of Man and Selection in Relation to Sex,* Darwin continued to compare the explanatory strength of the principle of direct adaption with that of the principle of natural selection. That is, he compared modification of an organ due to that organ's function and to the direct action of external conditions with accumulation of those hereditary variations which in the struggle for existence prove advantageous for given conditions of existence.

It is quite natural that Darwin's assertion that natural selection is more significant than direct adaptation as the active force of evolution, an assertion he repeated in various places in all three of his basic works, met with objections from proponents of the traditional transformist views associated with Lamarck's name. Opponents of Darwin could not reconcile themselves to the idea that the motive and directive force of evolution is the natural selection of random variations and that the theory of natural selection can easily account for evolution without the assumption of the inheritance of acquired characters.

Darwin carefully attended to all the commentaries he received, and he strove to make allowance for, or to refute with facts, the most prominent objections.

In the Preface to the second edition of the *Descent of Man,* Darwin primarily responded to critical comments he had received in his correspondence. "My critics," he wrote, "frequently assume that I attribute all changes of corporeal structure and mental power exclusively to the natural selection of such variations as are often called spontaneous; whereas, even in the first edition of the 'Origin of Species,' I distinctly stated that great weight must be attributed to the inherited effects of use and disuse, with respect both to the body and mind. I also attributed some amount of modification to the direct and prolonged action of changed conditions of life."[65]

[64] Darwin, "Letter to E. Krause, 28 November 1880," (n. 6) [Passage could not be located in the English.]

[65] Charles Darwin, *Proiskhozhdenie cheloveka i polovoi otbor* [*Descent of Man and Selection in Relation to Sex*], *Soch.* [*Works*], vol. 5 (1953), p. 121. [Passage follows the Preface in the second English edition (1874)].

In various passages in the *Descent of Man* Darwin, however, wrote with less certainty. Referring to the fact that "Different occupations, habitually followed, lead to changed portions in various parts of the body," he remarked, "Whether the several foregoing modifications would become hereditary, if the same habits of life were followed during many generations is not known, but it is probable."[66] He also wrote, "We may infer that when . . . the progenitors of man . . . were changing from quadrupeds into bipeds natural selection would probably have been greatly aided by the inherited effects of the increased or diminished use of different parts of the body."[67]

Darwin's proposals that habitual activities may influence the body's proportions and that the resultant changes may become hereditary was quite natural for that time, but he had at his disposal no experimental verification for such proposals.

What is surprising is that scientists quite seriously made such proposals even a century later. Thus, in his book *Habit and Heritage,* Frederic Wood Jones maintained that the facets on the lower end of the tibia bone and, correspondingly, on the upper surface of the calcaneus bone developed among the original inhabitants of Asia because of their habit of sitting on their heels.[68]

Jones's opinion was supported by anthropologists P. Huard and M. Montané,[69] who studied the structure of lower limbs in peoples of East Asia who have the custom of sitting on their heels. According to data of Huard and Montané, peculiarities in the feet of these peoples appear already in newborn babies and are expressed in them even more strongly than in adults. These authors found the same changes in prehistoric skeletons in Europe. Among modern Europeans, who use chairs, the adaptations to sitting on the heels are absent. Neither Jones nor Huard and Montané discussed the question: what, in this case, is the cause and what is the effect? Surely the habit of sitting on the heels did not cause a variation in the structure of the legs. Rather, a genetically conditioned peculiarity of the skeleton in ancestors of modern man and in certain peoples living now facilitated sitting on the heels. Such a solution to the problem, incidently, frees one from the necessity of explaining how such a variation in the legs could be adequately inherited.

Darwin said of his own vacillations in evaluating the relative significance of natural selection and direct adaptation, "in the earlier editions of my *Origin of Species* I perhaps attributed too much to the action of natural selection or the survival of the fittest. I have altered the fifth edition of the *Origin* so as to confine my remarks to adaptive changes of structure; but I am convinced, from the light gained during even the last few years, that very many structures which now appear to us useless, will hereafter be proved to be useful, and will therefore come within the range of natural selection."[70] Therefore, Darwin considered the concessions he initially made to proponents of direct adaptation as temporary, since he supposed that in the future the number of phenomena explainable on the basis of natural selection rather than inheritance of acquired changes would steadily expand. Meanwhile, he was obliged to apply the hypothesis of direct adaptation to those cases in which it had not been established that the new trait was advantageous and thereby subject to the action of natural selection.

Darwin devoted a number of pages in the *Variation under Domestication* to the question of the possible significance of use and disuse of organs and mechanical injury in the origin of morphological changes and in fixing those changes in progeny. But, as a rule, his opinions on this theme were not presented as categorical assertions.

The attempt to picture Darwin as an unreserved proponent of the inheritance of acquired characters prompted certain authors to cite his opinion on the recapitulation of ancestral traits during ontogeny, in particular, his statement that "at whatever period of life a peculiarity first appears, it tends to appear in the offspring at a corresponding age."[71] Darwin illustrated this rule with observations, such as the following example: the hereditary variations in the shape of horns that arose in ancestors of modern cattle become manifest only at a sufficiently late age when the horns are well formed. In other words, this is not a matter of when the trait originally appeared in the species, but when it appears in the individual. These statements by Darwin are sometimes interpreted arbitrarily. It should be noted that the interpretation of Darwin's words here may depend on the translation. In the quotation given above, the original verb "to appear" is translated sometimes by the word *proiavliat'sia* [to become manifest] and other times by the word *poiavliat'sia* [to appear, to originate]. These give rise to two interpretations. But Darwin quite clearly distinguished between the *appearance*, that is, the origin, of a trait and its *manifestation* at a certain age. He wrote, "The question is not at what period each change originates, but at what period the results of the change become manifest. The cause may operate, and I think often does operate,

[66] *Ibid.*, p. 159 [Passage follows authorized edition (New York: D. Appleton, 1897), p. 32.]
[67] *Ibid.*, pp. 161-162. [See English text, p. 35].
[68] Frederic Wood Jones, *Habit and Heritage* (London, 1943), p. 48.
[69] P. Huard and M. Montané, "Le squelette humain et l'attitude accroupie," *Bull. Soc. Etudes Indochin.* (Saigon, 1951), p. 26. Cited according to a lecture given by Franck Bourdier at a conference at the Sorbonne in September 1966, and published a year later (Bourdier, "Le lamarckisme et la raison," *Cahiers Rationalistes,* no. 252, pp. 1-14).

[70] Darwin (n. 65), pp. 132-133. [For English text see *op. cit.*, p. 61.]
[71] Darwin (n. 8), p. 279. [For English text see *op. cit.*, p. 13.]

on one or both parents even before the act of reproduction." [72]

We must then admit that Darwin's conceptions of recapitulation and of the timing of reproduction of ancestral traits in ontogeny were not actually based on the assumption of the inheritance of acquired characters.

Among Lamarckians at the end of the 19th century the idea of the inheritance by progeny of traits acquired by the parents was sometimes tied to the idea of the reproduction of these traits "at a corresponding age." Sometimes such ideas were based on completely untrustworthy observations, such as those cited by Theodor Eimer in his book, the very title of which reveals the author's intent to solve the whole problem of origin of species by starting from an assumption of inheritance of acquired traits. Eimer wrote: "I have observed that children born to very old parents, and especially to old fathers, even in early youth have faces that look aged." [73] Such "observations" require no comment.

[72] Darwin (n. 8), p. 631 [Corresponding English text could not be located.] This important passage from *Origin of Species* was commented on and Darwin's opinions correctly interpreted by Ivan Ivanovich Ezhikov in his article, "Uchenie o rekapituliatsii i ego kritiki" ["The Doctrine of Recapitulation and Its Critics"], included in the book: F. Miuller, *E. Gekkel'. Osnovnoi biogeneticheskii zakon. Izbrannye raboty.* [*E. Haeckel: The Fundamental Biogenetic Law: Selected Works*] (Moscow-Leningrad, 1940), p. 15.

[73] Gustav Heinrich Theodor Eimer, *Die Entstehung der Arten auf Grund von Vererben erworbener Eigenschaften nach den Gesetzen des organischen Wachsens* (Jena, 1888), p. 180.

CHAPTER 5

Ernst Haeckel and his Followers on the Inheritance of Acquired Characters

In contrast to Darwin, who, for his time, had demonstrated satisfactory scientific discretion with regard to the inheritance of acquired changes, Ernst Haeckel interpreted such changes in a categorical way. From the manner he cited the same examples as Darwin, even borrowing them directly from Darwin, one would have thought he had at his disposal proof not available to Darwin. Without reservation Haeckel attributed the underdevelopment of wings of domestic birds, the lop-earedness of domestic animals, etc., to a lack of use of the corresponding organs.

Haeckel had a penchant for detailed systematization of phenomena and concepts. In the second volume of his extensive work, *Generelle Morphologie,* he accordingly formulated "laws" of heredity. He first of all divided these into two basic groups: laws of conservation heredity (inheritance of innate characteristics) and laws of progressive heredity (inheritance of acquired characteristics). Haeckel enumerated four of the latter (in his overall list they appear as numbers six through nine). These laws reduce to the following:

"6. The law of adaptive, or acquired, heredity (*Lex hereditatis adaptivae* [*adaptatae*] *s. accomodatae*). [Both adjectives denote "accommodative", "adaptive"; in the Latin version of the law the concept "acquired" is absent—L.B.] All characteristics which the organism acquires in the course of its individual development through adaptation and which its forebears didn't possess, that organism can, under favorable circumstances, transfer to its progeny through heredity." [1]

Haeckel thought that all morphological or functional features acquirable by the individual as the result of the influence of the external environment, that is, all adaptations, could be transmitted to the progeny. He attached great significance to this law, which he called "great," for he believed that it accounted for the changes in species, that is, for the possibility of the origin of new species from already existing ones. Such inheritance, Haeckel believed, could be realized most easily in the situation in

[1] Ernst Haeckel, *Generelle Morphologie der Organismen,* 2 vols. (Berlin: Georg Reimer, 1866), vol. 2, p. 186.

which changes occur slowly and gradually, but he didn't exclude the inheritance of sudden, in particular, traumatic changes.

"7. The law of constitutive heredity (*Lex hereditatis constitutae*). All characteristics, which the organism acquires in the course of its individual existence through adaptation and which its forebears did not possess, will be inherited more precisely and completely in all following generations, the longer the causal conditions of adaptation act and the longer they act on successive generations." [2]

Haeckel attached great significance to this law also, since he considered it instrumental in the breeding of animals and plants. He was sure that any gardener could easily be convinced of the validity of this law. It seemed clear that of the newly arisen changes in animals and plants, the only ones that will be inherited and made constitutive are those that were evoked by repeated or prolonged influence, especially over the course of a series of generations. An organism, according to Haeckel, possesses a certain elasticity. He compared it to a metal rod which returns to its former shape if a bending force acts on it only momentarily. [On the other hand, if bent for a longer period of time, the rod will acquire a new shape—the editors]. Haeckel considered the law of constitutive inheritance so indisputable that he did not deem it necessary to give concrete examples.

"8. The law of heredity of the same location (*Lex hereditatis homotopae*). All organisms can transfer to their progeny definite changes of any part of the body which they acquire during their individual life through adaptation and which their forebears did not possess, precisely in the same form and in the same part of the body." [3]

This law too, as Haeckel thought, had such universal significance that its constant revelation did not evoke surprise. Although it was very difficult to imagine how the minute quantity of protein matter in the spermatozoid of the father and the ovule of the mother transfer for epigenetic development even minute changes in any part of the parent's body to the same part of its offspring (embryo or adult), Haeckel nevertheless thought that many facts were in accord with this law.

"9. The law of simultaneous heredity (*Lex hereditatis homochronae*). All organisms can transmit to their progeny at a comparable stage of life particular changes that they acquired through adaptation at any moment during their individual existence and that their forebears did not possess."

Haeckel claimed that Darwin first formulated this law under the name "Law of heredity at a corresponding age." He remarked that the action of this law may be observed so constantly that it is cause for little wonder and is not the subject of detailed investigation, yet the phenomena described by

[2] *Ibid.*, p. 187.
[3] *Ibid.*, p. 188.

this law "are among the most striking and difficult to explain of any phenomena observed in nature. Isn't it a striking yet well-known fact that a specific change experienced by the body of an organism at some moment of its life, is repeated at just that moment in its progeny? Isn't it also really amazing how the subtle molecular movements of plasma, which are the cause of such changes, are in the act of procreation transmitted via the sperm and egg from the parents to the organism of the offspring in such a way that for a specific period they don't become manifest in the offspring (that is, they remain in a concealed state) but become manifest only when the new organism attains that stage of life in which the parent organism acquired the change?" [4]

In his commentary on the eighth and ninth laws Haeckel admitted with touching helplessness that it is incredible how progeny undergo changes in exactly the same place and stage of ontogeny in which these changes arose in the parents. Nevertheless, Haeckel's *a priori* conviction of the necessity, or at least the unconditional possibility, of the inheritance of acquired characteristics, even of such changes as a one-time traumatic injury, prevented him seeing all the doubts concerning such a mode of inheritance and the inadequacy of the factual support of this concept. One will search in vain in the above mentioned work of Haeckel, or in his popular book, *History of Creation,* published two years later, for genuine evidence for the inheritance of acquired traits. Haeckel's reasoning ran like this: "It is my conviction, shared by many transformationists, . . . [that] the direct inheritance of new adaptations, in the Lamarckian sense, has immense significance, and comparative anatomy, ontogeny, physiology and pathology give thousands of examples of it." [5]

Haeckel used the same ancient method—inductive reasoning—as Lamarck and Darwin had used. As examples purporting to "prove" his laws, Haeckel listed a combination of incontestable instances of the inheritance of inherent traits, such as polydactyly, albinism, piebaldness, variegated leaf coloring, birthmarks, hirsuteness, and the like, and instances of the reappearance in offspring of diseases found in the parents. Some of these diseases are congenital by nature; some are the result not of inheritance but of infection from the parents.

A traumatic injury, in Haeckel's opinion, was usually not inherited. "How much more important then," he wrote, "to record those instances in which it does sometimes occur. For example, District Councillor Steckhart informed me with complete assurance that many tailless calves were

[4] *Ibid.*, p. 190.
[5] Ernst Haeckel, *Estestvennaia istoriia mirotvoreniia* [*History of Creation*], trans. A.G. Genkel' (St. Petersburg: 1913), p. 156. [*Natürliche Schöpfungs-geschichte* (Berlin: Georg Reimer, 1868.) Translation taken from the Russian.]

born not long ago on an estate near Jena. Their father had had his tail pinched and injured by someone carelessly closing the gate upon it."[6] Haeckel cited that very example in *The History of Creation* and added, without giving a direct reference, "It is said that a tailless race of dogs was obtained by cutting off the tails of both parents over the course of many generations."[7]

Wilhelm His
(1831-1904)

In his book *Unsere Körperform,* the embryologist Wilhelm His wrote on the same topic. "If acquired characters must be inherited then, of course, the question arises, is there not a necessary specific dependence of the embryonic matter on the individual parts of the parent [organism]? This would necessarily be so if characters were inherited which were acquired in the course of the individual's life, such as injuries to extremities or skills mastered through study. . . . For millennia we have stood and walked by one and the same means, for millennia. Our predecessors spoke in the same language and wrote in the same script, yet we ourselves and our children must learn these skills anew. For millennia various peoples have practiced

[6] Haeckel (n. 1), p. 187 n.

[7] Haeckel (n. 1), p. 157. [Translation taken from the Russian.]

circumcision, but the removed part has never disappeared through inheritance. This experience can outweigh a host of anecdotes listed in support of the inheritance of acquired characters." His made a footnote to this text in which he cited Haeckel's story about the bull with the injured tail having tailless offspring.[8]

It is not superfluous to recall that forty years before the publication of His's book, Karl Ernst von Baer, in a lecture given to the Physikalisch-ökonomischen Gesellschaft in Königsberg, expressed essentially the same understanding against the possibility of the inheritance of mechanical injury.

"From the point of view of procreation, people who have a leg cut off are just as complete individuals as animals which have a tail or ears cut short, since the children of the former are one-legged to no greater extent than the progeny of the latter are born into the world with foreshortened ears. . . . If you cut off the horns of your cows and bulls, their calves will nevertheless have horns. If you, however, cross a cow which is hornless by virtue of some inner predisposition (such individuals are found in certain places) with a similarly hornless bull, their progeny likewise will be hornless. From this it follows without doubt that those changes which are caused by accident or by some sudden external influence do not alter to the slightest degree the general type of the progeny. On the other hand, every divergence from the norm arising out of development of the individual itself will be transmitted in procreation."[9] Further on, however, Baer proposed, without supplying supporting arguments, that an external influence may, by changing the "manner of nurture" of the individual, "affect its reproduction" and exert an influence on "the following generations even when the original influence has ceased."[10] In all these discussions it is important to recognize the need to distinguish between non-inheritable changes which occur to the parents and hereditary changes "which arise during formation of the individual itself."

Emanuel Rádl, in his *History of Biological Theories,*[11] noted that Georg Seidlitz and Carl Nägeli were the first to establish a clear distinc-

[8] Wilhelm His, *Unsere Körperform und das physiologische Problem ihrer Entstehung* (Leipzig: F.C.W. Vogel, 1874), pp. 157-158, 223. [Translation taken from the original German. At this point His also quotes Bismarck attributing essentially the same story of a tailless dog to Count V. Arnim.]

[9] Karl Ernst von Baer, "Vseobshchii zakon prirody, proiavliaiushchiisia vo vsiakom razvitii" ["General Law of Nature Manifested in All Development"], *Izbrannye raboty* [*Selected Works*], ed. Yu. A. Filipchenko (Leningrad, 1924), p. 105. [First published as "Das allgemeinste Gesetz der Natur in aller Entwickelung," in *Reden gehalten in wissenschaftlichen* 3 vols. (St. Petersburg: H. Schmitzdorff, 1864-1873). Translation follows the German: vol. 1, p. 52.]

[10] *Ibid.*, p. 106 [*Ibid.*, p. 52.]

[11] Emanuel Rádl, *Geschichte der biologischen Theorien seit des siebzehten Jahrhunderts,* 2 vols. (Leipzig: 1905-1909), pp. 400-401.

tion between inherent and acquired characteristics. Nägeli [12] experimented on alpine varieties of plants. Even in the first generation after transplantation to a low altitude these plants lost traits which they had acquired in the mountains under the influence of an alpine climate. In other words, acquired traits were not inherited. Seidlitz, working on theoretical grounds, likewise doubted the inheritance of acquired traits. He objected to Haeckel's attempts to see in Nägeli's experiments a demonstration of evolutionary reversions and asserted that the latter could only be the result of inherent changes.[13]

Haeckel himself did not feel that his views were proven by rigorously verified facts. He confessed this in a letter to August Weismann who wholly rejected the inheritance of acquired characters. Congratulating his "deeply respected friend and colleague" on his sixtieth birthday on the 17th of January 1894, Haeckel expressed the hope that between himself and Weismann, "the old collegial and friendly relations would not be clouded" by scientific disagreement. "I consider the problem of progressive inheritance one of the most important in all biology, and besides, I am so firmly convinced of the inheritance of acquired characters that it seems to me that without it– and without its related 'phyletic adaptation'— evolutionary theory loses its explanatory significance. However, I willingly admit that at its foundation lies a philosophical 'matter of faith' and that convincing proof for it is just as scarce as for your contrasting view." [14]

Striving for consistency in the formulation of his view, Haeckel gave himself the task of imagining the possible mechanism of inheritance of acquired characters. Darwin's hypothesis of pangenesis did not satisfy him since the transfer of gemmules from all parts of the body and even from individual cells to the sex cells, in the light of data of microscopic anatomy, was simply not credible. In place of this hypothesis Haeckel proposed another, called "perigenesis of plastidules." In Haeckel's hypothesis, protein substance (plasson) of non-cellular structures and cells (plastids) are composed of molecules (plastidules) that possess the property of self-replication. Movement is inherent in plastidules. The peculiarities of the movement characterize a given cell and are transmitted, upon division, to the daughter cells. "Inheritance," in Haeckel's words, "is the transfer of the motion of plastidules, the distribution of individual molecular motion of plastidules from mother to daughter cells." [15] If daughter cells, initially

[12] Carl Wilhelm von Nägeli, *Entstehung und Begriff der naturhistorischen Art* (München: 1865).

[13] Georg Seidlitz, *Die Darwin'sche Theorie* (Leipzig: 1875). For more detail concerning the views of Seidlitz, see chapter 7.

[14] Georg Uschmann and Bernhard Hassenstein, "Der Breifwechsel zwischen Ernst Haeckel und August Weismann," *Jenaer Reden und Schriften* 1965: 53.

[15] Ernst Haeckel, *Über die Wellenzeugung der Lebensteilchen oder Die Perigenesis der Plastidule* (Berlin: 1876), p. 53. [Translation taken from the Russian.]

identical, end up in non-identical conditions, the motion of their plastidules changes, which in turn results in changes in the cells themselves, that is, in adaptations to the new conditions. These newly acquired traits of the cells are transmitted to their progeny. In the process of fertilization the forms of motion of plastidules of the egg and spermatozoon combine, which explains the resemblance of the organism to both its parents. Haeckel thought of the motion of plastidules as wave-shaped and called it perigenesis. He believed that reproduction of the form of motion upon its transmission from a given cell to its progeny depended on the memory of the plastidules. "Due to the memory of plastidules," wrote Haeckel, "plasson can transmit its characteristic traits from generation to generation through inheritance, and may add those which the plastids acquire through adaptation." [16] Somewhat later Haeckel repeated the same thought. "Inheritance is the memory of plastidules, and mutability is the capacity of plastidules for perception." [17] Louis Erlsberg had proposed an hypothesis of perigenesis of plastidules two years before Haeckel.[18] He thought that protoplasm was not homogeneous but consisted of molecular complexes that were incapable of reproduction and arose under the influence of their predecessors alongside them. Haeckel assumed the same manner of formation of new plastidules.[19] After the publication of Haeckel's paper on "plastidules," Erlsberg came out with a new report in which he used Haeckel's new term.

Contemporaries of Haeckel, starting with Darwin, regarded the hypothesis of perigenesis of plastidules very skeptically. Yves Delage, in his voluminous book on the structure of protoplasm and theories of inheritance as related to problems of general biology, noted the speculative character of Erslberg's hypothesis [20] and he reacted especially sharply to Haeckel's hypothesis of perigenesis of plastidules. Besides its mechanistic explanations of life phenomena, it contained, in Delage's words, "execrable metaphysical rubbish (exécrable fatras métaphysique), unworthy of naturalists of the present century." At Haeckel's bidding "a veritable phantasma-

[16] *Ibid.*, p. 68.

[17] *Ibid.*, p. 69. Haeckel's hypothesis is well presented in the book: Hans Stubbe, *Kurze Geschichte der Genetik bis zur Wiederentdeckung der Vererbungsregeln Gregor Mendels* (Jena: Gustav Fischer, 1963), pp. 131–133.

[18] Louis Erlsberg, "Regeneration, or the Preservation of Organic Molecules: A Contribution to the Doctrine of Evolution," *Proc. Am. Assoc. Adv. Sci.* (Hartford, Conn.), 1874, *23*, pt. 2: 87–103.

[19] If one wanted to seek in the history of science for "anticipation" of ideas expressed significantly later and on another empirical level, one might talk about Erlsberg and Haeckel's "anticipating" the concept of replication of structural components of protoplasm through matrix synthesis. In fact, talk of such anticipation is not justified here.

[20] Louis Erlsberg, "On the Plastitudle-Hypothesis," *Proc. Am. Assoc. Adv. Sci.* (Buffalo, N.Y.), 1876, *25*, pt. 2: 178–186.

goria of plastidules endowed with sensitivity, will, and memory swirls before the reader's eyes (Haeckel fait papilloter devant les yeux du lecteur toute une phantasmagorie).'[21] Haeckel's hypothesis indeed has a clearly speculative character. The endowment of plastidules with capacities of perception and memory puts this hypothesis in the same category as later constructions of the psycho-Lamarckians who refer to Haeckel as their predecessor.

Despite the lack of serious proof of inheritance of acquired characters, Haeckel for many years did not abandon his attempt to reconcile eclectically the Darwinian theory of natural selection with the Lamarckian assumption of direct adaptation caused by the animal's will. "By adapting to changes in the conditions of feeding by long-term habit, exercise, etc.," Haeckel wrote, "the will of animals can lead to extremely impressive alterations in organic form."[22]

Haeckel used the constructs and factual data of Wilhelm Roux to strengthen his own conviction. Roux had attempted in his early publications to construct a teleological principle by means of which function appeared in ontogeny earlier than form and created for itself the needed form. Roux's views were presented in a series of anatomical studies under the general title *Beiträge zur Morphologie der functionelle Anpassung*[23] and in his monograph *Der Kampf der Teile im Organismus.*[24]

In these works Roux's central idea was the notion of a so-called functional adaptation. According to Roux, organs, tissues, cells and even molecules of organic matter were found in the organism in a state of constant conflict with one another for food, space, and the utilization of external stimulation. In consequence the most adapted components of the organism prevailed and thus the most efficient structure of living beings came about. The source of improvement of parts was functional adaptation, which Roux defined as the ability of the entire organism and of its parts to adjust to voluntary and involuntary changes in habitual activity, that is, to the altered function. As a consequence the arrangement was altered, that is, so-called functional structures and functional forms, which were the immediate basis of organic harmony, were formed. In Roux's opinion functional adaptation was realized either by a trophic process (e.g., an increase in blood supply, by means of which newly arising mutations were established in phylogeny) or by a purely mechanical process (e.g., friction between joint surfaces, etc.).

[21] Yves Delage, *L'hérdité et les grands problèmes de la biologie général* (Paris: C. Reinwald, 1903), pp. 494-495.

[22] Haeckel (n. 5), p. 176. [Translation from the Russian.]

[23] Wilhelm Roux, "Beiträge zur Morphologie der funktionellen Anpassung," *Ges. Abhandl.*, 2 vols. (Leipzig: Wilhelm Engelman, 1895), I, 485-722.

[24] Wilhelm Roux, "Der züchtende Kampf der Teile oder die 'Teilsauslese' im Organismus, zugleich eine Theorie der funktionellen Anpassung," I, 135-422.

Nowhere in his papers, which were dedicated to functional adaptation and the conflict of parts in the organism, did Roux go on to clarify how the results of functional adaptation were transmitted to progeny. One need not be surprised at this since Roux did not have at his disposal a proof of inheritance of altered "functional structure." Nevertheless, basing himself on Roux's constructs, but not troubling himself to refer to any experimental data, Haeckel affirmed the inheritance of results use or disuse of organs.[25]

Haeckel's "laws of heredity" were not well received. Even authors inclined to explain evolution with the help of Lamarckian principles and therefore remaining close to Haeckel's views, reacted to his laws with great reservation. For example, we may refer to the famous Russian anatomist and popularizer of natural sciences, Pëtr Frantsevich Lesgaft, who published a lengthy article (over 170 pages) on "Heredity" in the journal *Russkoe Bogatstvo* [*Russian Wealth*]. Although he dealt little with inheritance proper, Lesgaft wrote about Haeckel's "laws." "One should in no way designate these propositions as laws," he insisted, "for they are insufficiently verified, and certain of them [the above-mentioned laws six through nine] are even now rejected by the majority of researchers."[26] After collecting the available factual data on the question of inheritance of acquired characters, Lesgaft made the following general conclusion: "Neither adaptation, nor the consequences of mechanical injury or alteration, nor deformities may be transmitted by inheritance; there may only be resemblances in consequence of similarity of conditions of development of the embryo."[27]

Haeckel's attitude toward the problem of inheritance of acquired characters was a "matter of faith" and not a matter of allowing or requiring a non-contradictory empirical solution. This was revealed in his unreserved support even of those views which, in essence, contradicted his generally materialistic point of view. In particular, Haeckel strongly supported the theory of Richard Semon, who began his scientific activity in the field of zoology under Haeckel's tutelage. Semon concerned himself with theoretical questions only later after moving from Jena to Munich. Haeckel's biographer, Georg Uschmann, using documentary evidence, testified that Semon "continued communication with Haeckel mainly in a

[25] Haeckel (n. 5), pp. 178-179.

[26] Pëtr Frantsevich Lesgaft, "Nasledstvennost'" ["Heredity"], *Russkoe bogatstvo* [*Russian Wealth*], no. 11, 1889, pp. 119-120.

[27] *Ibid.*, no. 12, p. 82.

discussion of the question of the inheritance of acquired characters, and in his theory of 'mnene' he [Semon] defended a neo-Lamarckian point of view. Haeckel maintained friendly relations with Semon to the end and (as is apparent from his letters) greeted Semon's hypothesis as the complement to his own views on 'progressive' inheritance.''[28]

Semon's views were not original. To a considerable extent they resurrected ideas expressed long before him by the physiologist Ewald Hering and the writer Samuel Butler. In his article ''On Memory as a General Function of Organized Matter,''[29] Hering started with the notion that any irritation, besides evoking a functional reaction, left some sort of trace in the structure of the organism. The aggregate of these traces, according to Hering, comprised what psychologists call memory. He postulated that such traces not only accumulate over the course of an individual's life but were transmitted to its progeny. In this way he equated the phenomenon of inheritance with memory. Butler developed analogous views in still greater detail, although with no better support from the scientific point of view, first in his book *Life and Habit*[30] and later in an outline of the history of evolutionary scientists.[31] As with Hering, Butler considered inheritance identical to memory and thought memory was the bridge between successive generations. According to Butler, the egg contained the consolidated memory, the accumulated experience of predecessors, which was reproduced in the developing embryo serially in the order in which each experience was acquired. Compelled by necessity, the individual repeated the same actions which thereby became habits. In consequence of the use of organs and the influence of the environment existing organs of the embryo developed more intensely, and previously absent structures may even appear. This combination of ideas, unsupported incidentally by any personal investigation, essentially reproduced in a vulgarized form the views expressed by Lamarck a hundred years earlier. Despite the fact that Butler's theory had the look of a genuine anachronism, it was recently sympathetically reviewed by Philip G. Fothergill in his neo-Lamarckian book on the history of evolutionary theories.[32]

[28] Georg Uschmann, *Geschichte der Zoologie und der zoologischen Anstalten in Jena, 1799–1919* (Jena: Gustav Fischer, 1959), p. 125. [Translation follows the German.]

[29] Ewald Hering, ''Über das Gedächtniss als eine algemeine Funktion der organisirten Materie,'' *Almanach d. k. Akad. d. Wiss.*, 1870, *20:* 20.

[30] Samuel Butler, *Life and Habit* (London: Trübner & Co., 1878).

[31] Samuel Butler, *Evolution, Old and New; or the Theories of Buffon, Dr. Erasmus Darwin, and Lamarck, as Compared with that of Mr. Charles Darwin* (London: Hardwicke and Bogue, 1879). This book was reprinted in 1882, 1890, 1911, and 1921.

[32] Phillip G. Fothergill, *Historical Aspects of Organic Evolution* (London: Hollis and Carter, 1952). A review of this book with indication of its non-objectivity and anti-Darwinian tendencies was published by Conway Zirkle (Conway Zirkle, in *Isis,* 1954, *54*).

The views of Hering and Butler have so little historical interest one could dispense with mentioning them if Semon, with Haeckel's blessing, had not tried to revive them. Semon's book is entitled *Mneme as the Conservative Principle in the Turnover of Biological Phenomena.*[33] Semon defined the term ''mneme'' (Greek for ''memory'') as the aggregate of all that is imprinted in the organism in the form of impressions, ''engramms,'' during the course of its individual life as well as impressions inherited from predecessors, which in their turn acquired similar engramms under the influence of external stimulation. Because of Haeckel's concepts of the perception and memory of plastidules, Semon included him on the list of his predecessors, which also included Hering, Butler, F. Thomas Laycock, and Henry B. Orr. The factual side of the problem of the inheritance of acquired characters, the assumption of which is an organic and integral part of Semon's hypothesis, remains practically unsupported in his book. Semon merely listed those authors (L. Blaringheim, Georg Klebs, E. Bordage, Paul Kammerer, and others) who published experimental results which he thought confirmed the inheritance of acquired traits. He did not bother to examine the experiments or evaluate their degree of validity.

Soon after Semon's book was published, August Weismann wrote a critical review of it in which he touched upon the identification of heredity with memory as well as the factual basis required for Semon's theory.[34] Weismann objected to Semon's conception of the transmission of ''engramms'' from various parts of the soma to the sex cells via the peripheral nervous system. He argued that nerve paths were not railroads along which all possible stimuli could be transported in any direction. It was impossible to imagine that specific stimuli were carried along the nervous system to a predetermined unloading site of the embryonic substance and that they caused a like engramm there. Weismann considered unconvincing the attempt which Semon made at a factual confirmation of the inheritance of somatogenic traits. Since there exist a host of traits whose genesis depends on immediate changes of the germ-plasm, Weismann argued that there was no cause to seek some other explanatory principle for other traits.

Valentin Haecker spoke out on the fundamental principle, the analogy between heredity and memory, employed by Semon and his predecessors.[35] He compared the sequence of events which must take place for the

[33] Richard Semon, *Die Mneme als erhaltendes Prinzip im Wechsel des organischen Geschehens* (Leipzig: 1904). See also Richard Semon, *Das Problem der Vererbung ''erworbener Eigenschaften''* (Leipzig: 1912), p. 20.

[34] August Weismann, ''Richard Semons 'Mneme' und die 'Vererbung erworbener Eigneschaften''', *Arch. Rassen-und Gesellschaftsbiol.*, 1906, *3:* 1–27.

[35] Valentin Haecker, *Über Gedächtnis, Verebung und Pluripotenz* (Jena: Gustav Fischer, 1914).

inheritance of acquired characters, assuming such inheritance, with the sequence of events which must go into the fixing of impressions in the memory. Haecker's conclusion reduced to the proposition that between these two series of processes there is but a superficial resemblance and that there is no justification to equate them. Yurii A. Filipchenko made analogous critical comments on mnemic theories of heredity in his book dedicated to the history of evolutionary views. [36]

The English Lamarckian, Ernest W. McBride developed a concept of evolution similar to the "mnemic" one. In one of his articles in the early thirties McBride called habit "the driving factor of evolution." [37] In his opinion, admission of the fact of evolution itself derives from a teleological analysis of the habits of evolving animals. McBride's thought process was this: "Since changed habits, by exercising different parts of the body, do modify structure, and since we know that animals can and do change their habits in response to the demands of a changed environment, it is a natural inference that the changed habits are the cause of the changed structure, and that the structural response on the individual has finally become engrained in the heredity of the race. So strong is the evidence for this inference, that some of my friends among the leading systematists of the British Museum deny altogether the necessity for direct experimental confirmation of it, arguing, with probable justice, that so many generations would be needed to make the change manifest that the time required would far exceed the span of an experimenter's life." [38]

Fothergill cited with full sympathy this reasoning of McBride which closes the door to an objective study of the question of the inheritance of acquired characters. Fothergill's own conceptions of evolution are clear from his perception of Darwinism. He expressed regret that "Darwin's book was published at a time that might be called the golden era of materialism." Darwin's theory "excluded teleology and thereby limited the realm of generalization," at a time when, according to Fothergill's own views, evolutionarv theory must be based on teleological grounds. J.W. Heslop Harrison, to whom Fothergill dedicated his book, spoke out still more decisively on this in the foreword to the book. Harrison thought a man of definite religious views could discuss questions of evolution without detriment to his religious beliefs. Naturally, he would have to adhere to Lamarckian, that is to teleological concepts. "On *a priori* grounds then,"

[36] Yurii Aleksandrovich Filipchenko, *Evoliutsionnaia ideia v biologii. Istoricheskii obzor evoliutsionnykh uchenii XIX veka* [*The Evolutionary Idea in Biology: An Historical Outline of Evolutionary Teachings of the 19th Century*] (Moscow: 1923).

[37] Ernest William McBride, "Habit: The Driving Force of Evolution," *Nature*, 1931, *127:* 933-944.

[38] [Ernest William McBride, "The Inheritance of Acquired Characters," *Nature*, 1932, *129:* 900. The quotation also appears in] Fothergill (n. 32), p. 255.

wrote Fothergill, "Lamarckism is an ideal and acceptable causal theory of evolution. . . . but on *a posteriori* grounds it lacks confirmation." [39]

Among Haeckel's followers who incidentally did not share his psycho-Lamarckian notions, we ought to mention his successor in the chair of zoology at Jena, Ludwig Plate. Like Haeckel, Plate thought that Darwinism "consists of two elements: Lamarckism and selectionism." Plate divided the post-Darwinian evolutionary theories into three groups: first, strict Lamarckism, the proponents of which either entirely rejected the significance of natural selection or assigned it subordinate significance; second, neo-Darwinism, the proponents of which conversely rejected "the Lamarckian component of Darwinism—inheritance of changes acquired by utilization or in consequence of manner of life (somatogenic changes)—and admitted only variations of inherited substances." [40] The third point of view, which Plate himself defended, was essentially that Darwinism should be preserved in its original form. Thus, according to Plate, one should accept the principle of selection as well as the Lamarckian principle of direct adaptation by the inheritance of acquired characters. In Plate's book cited above, the arguments which favor the inheritance of acquired characters are examined rather minutely. Plate seems to proceed from a perfectly correct understanding of concepts, maintaining that "under the inheritance of an acquired character one must keep in mind that a new trait has in the first generation a somatogenic, and in all succeeding generations blastogenic, origin." [41] Plate justly thought that "in the instance of a new trait obtained by experimental means, it must be shown that it is reproduced to a lesser extent in the F_2 even when the evoking stimulus did not act on the F_1, since identical changes in the P and F_1 might depend on the fact that under the influence of the effective stimulus, the cytoplasm of both somatic and sex cells of the P is adequately altered." [42] According to his hypothesis, external stimulation alters determinants of the germ-plasm which, in answer to this influence, are altered in the same direction as the somatic determinants. Plate could not see how unsatisfactory the factual arguments for somatic induction were. His main fund of supporting evidence was Kammerer's experiments, the validity of which was not yet the subject of much doubt. Plate saw a way out of all these difficulties as follows: stimulations transmitted by the altered soma to the sex cells are very weak in the sense that the stimulus must act on the soma over the course of many generations for alterations to be perceived in the sex cells.

[39] Fothergill, *ibid.*, p. 163.

[40] Ludwig Hermann Plate, *Selektionsprinzip und Probleme der Artbildung Ein Handbuch der Darwinismus* (4th ed.; Leipzig u. Berlin: W. Engelmann, 1913), p. 10.

[41] *Ibid.*, p. 493.

[42] *Ibid.*, p. 494.

"This points out the impossibility, or at least the very small probability, of obtaining experimental proof of functional inheritance,"[43] that is, the inheritance of the results of use or disuse of organs. Plate explained the noninheritability of mechanical injury thus: the removal of a part of the body with its complement of "somatic determinants" means that the latter can "no longer transfer stimulations to the corresponding determinants in the sex cells, much less eliminate those determinants. It is precisely this elimination which is necessary in order to hinder the development of the removed organ in the next generation."[44]

Naturally, such speculative reasoning had little effect in promoting those eclectic attempts to combine the Darwinian conception of evolution by natural selection with the Lamarckian conception of evolution by direct adaptation.

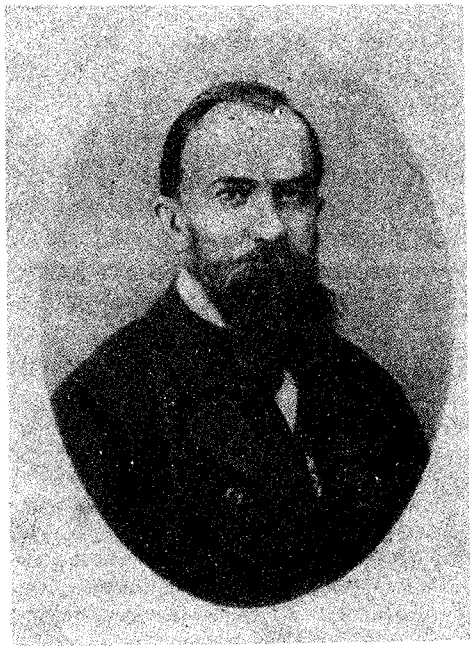
[43] *Ibid.*, p. 495.
[44] *Ibid.*, p. 496.

CHAPTER 6

Paleontologists's Views on the Question of Inheritance of Acquired Characters

It is difficult for the historian to explain the fact that quite a few *a priori* judgments in favor of inheritance of acquired characters were expressed, especially at the end of the nineteenth century, by paleontologists, that is, by representatives of that field of biology which cannot claim proof of such assertions. At times, however, one must reckon not with the opinions of the paleontologists themselves but with the allegations made by recent commentators on their work.

This applies, first of all, to the founder of evolutionary paleontology, Vladimir Onufrievich Kovalevsky. As he set about the study of fossil



Vladimir Onufrievich Kovalevsky
(1842–1883)

remains of mammals, Kovalevsky was already equipped with Darwin's theory, and during the whole of his brilliant scientific career, which was prematurely terminated, he maintained an unshakeable faith in the correctness of the Darwinian theory of evolution based on the principle of natural selection. He considered Darwinism not one among several possible viewpoints, including Lamarck's evolutionary belief—the theory of evolution "by means of the slow will of animals," as Darwin termed it—but as the only scientific principle capable of explaining materialistically the regular succession of animal forms which inhabit the earth.

Kovalevsky decisively objected to any attempts to replace Darwin's teaching by any other theory, and in particular he opposed "the degrading of this doctrine from the status of a scientific theory to the status of the Lamarckian proposition." [1]

Investigators of the scientific papers of Kovalevsky and his biographers Aleksei Alekseevich Borisiak and Leo Shiovich Davitashvili recognized that Kovalevsky was a confirmed Darwinist although they themselves did not consistently defend the same point of view. To make clear the genuine evolutionary views of Kovalevsky we need to examine those statements of his that authors sometimes cite when they falsely attribute to him Lamarckian views. It is essential to examine Davitashvili's appraisals of Kovalevsky's scientific views since these appraisals, expressed at various times, are clearly at odds with one another.

In a book dedicated to the history of post-Darwinian paleontology, [2] and in the first edition of his biography of Kovalevsky, [3] Davitashvili correctly objected to the opinion of Lamarckian paleontologists Rudolf Hoernes, Karl Diener, Othenio Abel and others. All of these had looked upon Kovalevsky as "the forerunner of the original founders of neo-Lamarckism in the field of paleontology," Edward Drinker Cope and Henry Fairfield Osborn. [4] Diener in particular had attributed to Kovalevsky the creation of the neo-Lamarckian theory of kinetogenesis, [5] the author of which was actually Cope.

[1] Vladimir Onufrievich Kovalevskii, *Osteologiia Anchitherium aurelianense Cuv. kak formy, vyiasniaiushchei genealogiiu tipa loshadi (Equus)* [*Osteology of Anchitherium aurelianense Cuv., a Form Which Clarifies the Genealogy of the Horse (Equus)*] (Kiev, 1873), rept. in the book: V.O. Kovalevskii, *Paleontologiia loshadei* [*Paleontology of Horses*], ed., L. Sh. Davitashvili (Moscow, 1948), p. 168.

[2] Leo Shiovich Davitashvili, *Razvitie idei i metodov paleontologii posle Darvina* [*Development of Ideas and Methods of Paleontology After Darwin*] (Moscow, 1940), pp. 32–46.

[3] Leo Shiovich Davitashvili, *V.O. Kovalevskii* (Moscow, 1946), pp. 192–290.

[4] Rudolf Hoernes, *Das Aussterben der Arten und Gattungen sowie der grösseren Gruppen des Tier- und Pflanzenreiches* (Graz: Leuschner & Libensky, 1911), (Quotation translated from the Russian.)

[5] Davitashvili (n. 2), p. 41.

Davitashvili convincingly demonstrated how foreign such views were to Kovalevsky. As he wrote, "The Darwinist Kovalevsky, who with unsurpassed mastery applied Darwin's theory to the study of fossil organisms, is fashioned a Lamarckist by many leading scientific figures, though there are absolutely no features of Lamarckism or neo-Lamarckism in his work." [6] "In V.O. Kovalevsky's works we do not find a single instance which would give us the right to speak of an inclination on his part toward any variety of neo-Lamarckism or Lamarckism." [7] An introductory section to the ninth chapter of this biography is [significantly] entitled, "The Supposed Neo-Lamarckism of V.O. Kovalevsky."

These opinions were clearly argued with reference to the appropriate passages in the works of Kovalevsky. For example, Davitashvili concluded that "V.O., in all his paleontological studies, analyzes the problem of the factors of evolution, and he does so always from the point of view of natural selection." [8] Such a conclusion can indeed be supported by numerous excerpts from the work of Kovalevsky. Thus, for instance, Kovalevsky explained the evolution of the skeleton of limbs in the transition from polydactyl ancestral forms to the monodactyl modern horse. This evolution was not the result of a lack of exercise of the diminishing digits, but the result of natural selection, which eliminated the "less economically" (Kovalevsky's expression) structured form with its complex limbs and guaranteed the survival of the form with the simplified structure in the skeleton of its limbs.

The persuasiveness of Kovalevsky's evolutionary generalizations depended on his consistent application of the principle of unity of form and function. In his work "Monograph on the Genus *Anthracotherium*," Kovalevsky characterized the reduction of the skeleton of the limbs in the evolution of the swine, which came about by the exaggeration of metapodia III and IV and their adaptation to bearing the weight of the whole body. This development of two metapodia was connected, according to Kovalevsky, to an "increase" in their function. With the enlargement of metacarpals III and IV their functional-morphological relation to the bones of the carpus simultaneously changed. "Consequently," wrote Davitashvili, "the intensification [of function] here is inseparable from other functional-morphological changes." [9] The same unity of changes in form and function was illustrated by Kovalevsky in his example of the molarization of premolars (that is, their assumption of the form of the more complex molars) in ungulates. "Simultaneously with the change in form," wrote Davitash-

[6] *Ibid.*, p. 41.

[7] Davitashvili (n. 3), p. 199.

[8] *Ibid.*, p. 204.

[9] *Ibid.*, p. 268.

vili, "there occurred a definite change in basic functions: . . . instead of biting, their primary function became mastication." [10] Kovalevsky also cited the development of the pulley-like form of the articulating surface of the lower end of the humerus in ancestors of the horse as an illustration of the [same] principle of unity of form and function.

Kovalevsky showed just as clearly in other examples that changes in function, which arose in altered conditions of existence and which promoted survival [of the organism] in these new conditions, are possible only with the simultaneous appearance of the morphological changes which support that function. These morphological changes might be hardly noticeable but were sometimes discovered on objects studied by paleontologists. In particular, Kovalevsky cited the example of the development of a facet on *os unciformis,* which in paleotherians is "positioned so obliquely that metacarpal III only slides across it, not being supportable on [the unciform]. . . . Turning to anchitheria, we note an interesting change: the facet has a less oblique position and already can offer some support to metacarpal III." Kovalevsky wrote further that in hiparrion this facet is "much larger and significantly less oblique," so that metacarpal III "already begins to rest firmly on the unciform." [11] Increase in the pressure of one bone resting on another was possible, therefore, only in the case that there was something to rest on; thus the function of bones changed simultaneously with their change in form. Concerning the origin of the pulley-like form of the articulating surface of the lower head of the middle carpal bone in the ancestors of the horse, Kovalevsky wrote, "There is no doubt that this alteration developed gradually over many generations . . . but each individual in which this extension of the lower head was more strongly expressed, possessed with it an advantage over others and had a high probability of transmitting this trait to its descendants." [12] The meaning of these words of Kovalevsky is unequivocal. The strengthening of the joints (their pulley-like form), which made movement possible only in the vertical plane, allowed the horse to get along with a single middle digit; at the same time the lateral digits became superfluous and were eliminated by natural selection. In connection with this view of the motive force of the evolutionary process Kovalevsky nowhere speaks of exercise or non-exercise as factors in the evolutionary transformation of limbs.

If in the first edition of his biography of Kovalevsky, Davitashvili consistently refuted accusations of Kovalevsky's adherence to neo-Lamarckism, in the second edition he was concerned only that Kovalevsky should not be considered an autogeneticist or psycho-Lamarckian.

[10] *Ibid.*, p. 269.
[11] Kovalevskii (n. 1), p. 201.
[12] *Ibid.*, p. 115.

In a study of the evolution of the skeleton of the antebrachium in the ancestors of the horse, Kovalevsky had spoken of the coordinated change in function and structure. Davitashvili cited this example and added the following phrase to his second edition: "Here it is perfectly clearly shown that function plays a leading role in the morphological development of organs." [13] Prior to this statement, then several pages further on, and once more at the end of his book Davitashvili repeated the same claim. "Kovalevsky indeed proved the dependence of form on function and the leading role of function in the evolutionary (phylogenetic) development of the structure of organs." [14] "Kovalevsky proved that in the interrelated changes of function and organs, *function plays the leading role.*" [15] "He [Kovalevsky], as we have seen, proved that in the evolution of organs and their functions changes in function play the leading role." [16]

In all of these statements the word "proved" is found, but nowhere is it said what cognitive operation is meant by this word. The author doesn't make it clear by what method, other than the experimental method, unavailable to paleontology, one may convincingly prove that the function of organs in predecessors influences the development of those organs in descendants. The expression "leading role of function in phylogenesis," devoid of concrete biological content, seems a verbal substitute for the Lamarckian thesis which postulates the dependence of the development of organs on their greater or lesser use and the inheritance of the results of the corresponding changes.

[By means of brackets we may further contrast the additions made to the second edition of Davitashvili's biography.] Concerning Kovalevsky's data on the extension of the first phalanx of the middle digit in predecessors of the horse, Davitashvili wrote, "A decisive role in this process should be attributed to [exercise and] selection for length of the first phalanx of the middle metapodium. In the instance just examined Kovalevsky clarifies not only the phylogenetic changes of organs and functions, but also the consecutive stages of these changes [as well as the significance of exercise] and the role of natural selection in the development of separate elements." [17]

In the conclusion to the paragraph just quoted, it was again stated: "Kovalevsky doesn't confine himself to establishing the mere fact of changes of organs and their functions; he also examines the reasons for these changes, explaining how in each separate instance natural selection

[13] Leo Shiovich Davitashvili, *V.O. Kovalevskii* (2nd ed.; Moscow: 1952), p. 392.
[14] *Ibid.*, p. 264.
[15] *Ibid.*, p. 398.
[16] *Ibid.*, p. 535.
[17] *Ibid.*, p. 396. The words in brackets are those missing from these phrases in the first edition of the book (pp. 275–276).

was at play, [and what role the exercise (or lack of exercise) of organs played]."[18]

Davitashvili made a still more decisive revision of Kovalevsky's evolutionary views in a special article in which he set himself the task of showing the allegiance of Russian paleontologists of the prerevolutionary period to the idea of the inheritance of acquired characters. This idea he unreservedly called "one of the basic premises of materialistic biology."[19]

Davitashvili arbitrarily dealt with quotations as he referred to Kovalevsky's statements that the structure of the teeth in herbivorous mammals changed concommitantly with their switch to the eating of grass. He interpreted the conclusions drawn from these observations as evidence that Kovalevsky assumed a direct influence of the type of food and manner of its mastication on the evolutionary changes in the tooth pattern. Completely without grounds Davitashvili asserted, "Kovalevsky assumed that evolution is accomplished through deviations evoked by the influence of external conditions, which is equivalent to assuming the inheritance of acquired characters."[20] And in another passage, "Kovalevsky based his position concerning adequate function on the abundant paleontological material, and he proceeded from the idea that traits which arise in the process of functioning are inheritable."[21]

The first of these last two excerpts testifies that the author of these words equated without foundation two completely different phenomena. Thus he confused the direct (mutagenic) or indirect (via natural selection) influence of the environment, on the one hand, with inheritance of phenotypic changes brought about by external influences, on the other.

Earlier Davitashvili himself had held another, completely correct view of the motive force of evolution. The criticism he made of Cope's "kinetogenesis" illustrates this: "Alterations in organs and tissues brought about in the parents by exercise or lack of exercise of organs . . . does not bring about adequate changes in the sex cells of the parents, and this means that they do not lead to the appearance of similar somatic alterations in the offspring. It follows that kinetogenesis as a factor in evolution is refuted by modern science."[22]

The outcome of our examination of Kovalevsky's genuine evolutionary views should be the conviction that he was averse to a Lamarckian interpretation of the role of external influences and functions in the phylogenetic changes in organs. As was shown above, and as Davitashvili asserted earlier, Kovalevsky considered the Darwinian principle of natural selection to be the motive force of evolution.

[18] *Ibid.*, p. 398. In brackets—words not included in the first edition (p. 276).

[19] Leo Shiovich Davitashvili, "Ideia nasledovaniia priobretennykh organizmom priznakov v russkoi paleontologii (do 1917 g.)" ["The Idea of the Inheritance of Acquired Characters in Russian Paleontology (before 1917)"] *Tr. In-ta istorii estestvozn.* [*Annals of the Institute for the History of Natural Science*], vol. V, 1953, p. 92.

[20] *Ibid.*, p. 66.

[21] *Ibid.*, p. 69.

[22] Davitashvili (n. 2), p. 91.

The Lamarckian tendencies of some German and many American paleontologists of the end of the nineteenth and beginning of the twentieth century is an indisputable fact.[23]

In particular, Melchior Neumayr, while considering the motive force of evolution to be natural selection, also allowed participation of the direct influence of the environment, in the evolutionary process. In his opinion, the environment could induce adequate inheritable changes. Neumayr backed up this idea with a mistaken belief in the inheritance of accidental injuries, which he uncritically considered "indisputable examples of the inheritance of acquired traits."[24]

One of the first paleontologists to defend Lamarckian concepts consistently was Cope. In his opinion, inheritable traits could arise as the result of mechanical influences caused by the movement (exercise) of organs (kinetogenesis), as well as under the influence of physical and chemical agents of the external environment (physiogenesis). The phenomena of kinetogenesis Cope attributed mostly to animals; those of physiogenesis to plants. Cope's discussion remained on the same scientific level as the corresponding "proof" offered by Lamarck. Even the examples Cope used resembled Lamarck's. He made use of secondhand accounts. He asserted, for example, that inflammation in the eye of a brood-mare led to the birth of a foal blind in the same eye; that when chickens, earlier having normal offspring, were mated with a fighting cock which had been blinded in one eye, they gave one-eyed chicks; and that a woman with an injured patella bore a child with the same defect.

Cope imagined the development of horns on the posteriolateral corners of the skull and on the nose in reptiles and mammals to be the result of blows from defense and offense. Furthermore he felt that excess bony and horny matter was formed in the places which experienced this external pressure.[25] As a paleontological "proof" of the inheritance of acquired traits Cope also offered the example communicated by Alpheus Hyatt,

[23] The neo-Lamarckian views of American paleontologists of this particular period are illustrated in Alpheus Spring Packard, *Lamarck; The Founder of Evolution: His Life and Work* (New York: 1901) and in the following articles: Robert Scoon, "The Rise and Impact of Evolutionary Ideas," *Evolutionary Thought in America* (New Haven: Yale University Press, 1950), pp. 4–42; Edward J. Pfeifer, "The Genesis of American neo-Lamarckism," *Isis*, 1965, *56*: 156–167.

[24] Melchior Neumayr, *Die Stämme des Tierreiches* (Wien u. Prag: 1889), p. 126. [Translated from the Russian.]

[25] Edward Drinker Cope, *The Primary Factors of Organic Evolution* (2nd ed; Chicago: Open Court, 1904), p. 314.

which was reproduced several times in other neo-Lamarckian compositions, including that of Felix-Alexandre LeDantec. The proof concerns the concave zone of the spiral shell of fossil cephalopods (nautiloids and ammonoids), the appearance of which Hyatt attributed to the pressure of adjacent turns of the spiral. In phylogenetically more recent forms the concavity of the shell sometimes appears even in those shells whose spiral turns have stopped touching one another.[26] Cope considered this example convincing evidence of the inheritance of the results of mechanical influence although he formed this assertion guardedly ("the mechanically acquired zone apparently is transferred by inheritance")[27] LeDantec had already proclaimed Hyatt's discovery without reservation as an "irrefutable proof of the hereditary transfer of acquired traits."[28]

Karl Zittel made the same inference in the textbook *Fundamentals of Paleontology* (in the sixth German edition of 1924). This inference was preserved in the Russian edition (the corresponding section in it was rewritten by Nikolai Ivanovich Iakovlev) and is accompanied by the conclusion that "In general, we may say that paleontology speaks in favor of the theory of the inheritance of acquired characters."[29]

To explain the mechanism of reproduction in offspring of changes arising in their predecessors, Cope resorted to the theory of diplogenesis. The core principle of this theory was a two-fold (thus the name of the theory) action of change-producing agents, that is, on the somatic part of the organism and on its germ-plasm. Thus, rather than accepting that a new trait acted in a way sufficient to change the germ-plasm, Cope maintained that under the influence of one and the same agent there took place a simultaneous and sufficient alteration of the soma and the germ-plasm. Davitashvili noted that Cope's hypothesis is close in meaning to the notion of parallel induction. "The latter," as he justly concluded in his book of 1940, "is also not (empirically) supported and not credible since it is extremely difficult to visualize how a factor which caused a certain change in an organ could cause a complementary change in the sexual elements."[30]

From his early works, published in the late 1860s, to his book of 1896 mentioned here, Cope continued to adhere to the opinion that

[26] Alpheus Hyatt, "The Phylogeny of an Acquired Characteristic," *Proc. Amer. Phil. Soc.*, 1894, *32:* 349–647.

[27] Cope (n. 25), p. 420.

[28] Felix-Alexandre LeDantec, *Individual'naia evoliutsiia, nasledstvennost' i neodarvinisty* [*Evolution individuelle et l'hérédité, théorie de la variation quantitative*] (1898) (Moscow: 1899), p. 157.

[29] Karl Alfred von Zittel, *Osnovy paleontologii* [*Fundamentals of Paleontology*], reworked under editorship of A.N. Riabinin (Moscow-Leningrad: 1934), p. 27.

[30] Davitashvili (n. 2), p. 92.

natural selection played a secondary role in the process of evolution, and he placed much greater weight on the action of a special factor which directed evolution via inheritance of acquired characters. Cope gave this factor the name "bathmism" or growth power, so as to distinguish it, above all, from forces of a non-biological nature.

According to Cope, the influences directing the activity of this growth force are various; among them he included the physical and chemical influences of the environment, the use of organs, reactions to necessity, and finally, conscious choice. Later Cope gave even greater significance to the last of these influences by including memory as a motive agent in evolution. His attraction to psychological concepts in order to explain the evolutionary process puts Cope close to other representatives of the vitalistic wing of neo-Lamarckians.

In regard to Lamarckian views of paleontologists and the factual data on which these views are based, Mikhail Aleksandrovich Menzbir correctly remarked that the material presented by Cope and others "in and of itself says nothing for or against the teachings of Lamarck or Darwin. Such material only proves that the vertebral column went through an evolutionary development, while clarification of the laws of this development requires the study of extant animals and a more profound understanding of the very essence of phenomena of evolution. This is best demonstrated by the fact that . . . V.O. Kovalevsky, proceeding from Darwin's teachings, gave a brilliant picture of the evolution of ungulates. He demonstrated the difference between adaptive and nonadaptive forms, explaining why some come out victors and survive in the battle for existence, while others die off, and thus he showed what scientific paleontological research, based on Darwinian principles, can truly provide."[31]

Hyatt's and Cope's successor was the famous American paleontologist Osborn, who at first espoused the basic principles of Lamarckism. One of his pertinent papers is entitled "Paleontological proof of the transfer of acquired traits."[32] In it Osborn discussed the question of the mechanism of the origin of tooth cusps in predecessors of the horse; these cusps, in his opinion, arose in the form of such small rudiments that they had no adaptive value and therefore were not eliminated by natural selection. The enlargement of these cusps, Osborn proposed, could be explained by enlisting the Lamarckian principle of the inheritance of results of exercise, which led to the creation of an adaptive, efficient tooth structure. Soon, however, under the influence of the work of Weismann, who criticized the

[31] Mikhail Aleksandrovich Menzbir, *Za Darvina* [*For Darwin*] (Moscow-Leningrad: 1927), pp. 92–93.

[32] Henry Fairfield Osborn, "The Paleontological Evidence for the Transmission of Acquired Characters," *Amer. Naturalist,* 1889, *23:* 561–566.

theory of inheritance of acquired characters, Osborn came to doubt the correctness of Lamarckian teachings. He expressed these doubts in a speech, "Are acquired traits inherited?" delivered at the opening of a symposium on the Lamarckian principle of evolution during the convention of the American Society of Naturalists in 1890. Osborn maintained that this principle could not possibly explain all of the phenomena that evolution comprises. He also referred to the opinion of Edwin Ray Lancaster who, in agreement with Weismann, asserted that there was no convincing proof of the Lamarckian principle of the hereditary transfer of acquired traits. Therefore, until such a proof was found, the second law of Lamarck could not be considered true. Later Osborn discussed the theoretical possibility of the inheritance of acquired traits. In his words, "inasmuch as sex cells usually are differentiated and separated from somatic cells at an early age, it is difficult to imagine how certain changes in this or that peripheral somatic cell, arising in adults of higher Metazoa, could evoke such changes in the sex cells that [these changes] would be reproduced in offspring, even if for this process we assume a very long time."[33]

Subsequently Osborn attempted to form a compromise theory, taking into account various factors in the evolutionary process. He felt there were four such factors and therefore spoke of the law of tetraplasia. According to this, evolution depends on: the factor of Buffon (direct influence of the environment), the factor of Lamarck (influence of ontogenetic changes, arising as the result of exercise of an organ), the factor of Darwin (natural selection), and the autogenetic factor of inheritable variability.[34] At the end of his scientific career in the 1930s, Osborn placed greater and greater significance on this last factor. Ultimately he broke with Lamarckism as well as Darwinism and emphasized the far from novel autogenetic concept of aristogenesis. By aristogenesis he meant the creation of new traits during blastogenesis, which resulted in greater and greater adaptation to the conditions of existence. For an evaluation of the methodological and scientific significance of these teleological ideas of Osborn, it is sufficient to offer his own words: "Aristogenesis is a completely inexplicable and mysterious process."[35]

Thomas Hunt Morgan vigorously opposed the paleontologists who advanced Lamarckian views. In his book *Evolution and Adaptation,* he wrote, "Certain naturalists, especially of the American school, are inclined to assert that the evolution of certain groups can best be explained by the theory of inheritance of acquired traits. . . . Despite the great number of

[33] Henry Fairfield Osborn, "Are Acquired Variations Inherited?" *ibid.,* 1891, *25:* 209.

[34] Henry Fairfield Osborn, "Tetraplasy, The Law of the Four Inseparable Factors of Evolution," *J. Acad. Nation. Sci.,* 1912, special anniversary volume: 275-309.

[35] Henry Fairfield Osborn, "Aristogenesis, The Observed Order of Biomechanical Evolution," *Proc. Nat. Acad. Sci. USA,* 1933, *19:* 260.

Thomas Hunt Morgan
(1866-1945)

examples listed, concerning which it might seem that the simplest explanation would be acceptance of inheritance of acquired traits, proof that such inheritance is possible does not exist. Why not use even a small part of the energy spent on theoretical discussion to demonstrate that this thing is actually possible. One of the merits of the Lamarckian theory is that it is accessible to experimental verification, and from whom can we expect this verification if not from neo-Lamarckists?"[36]

This completely just comment could be addressed to paleontologists only in an ironical sense since by the very character of paleontology one cannot apply the experimental method.

Morgan wanted to remind paleontologists in a polite manner that even discussion, much less resolution, of the question of the inheritance of acquired traits extends beyond the limits of their competence.

Several others (E.F.K. Koken, O.M.J. Jaeckel, *et al.*), including certain Russian paleontologists, tended toward a Lamarckian explanation of the

[36] Thomas Hunt Morgan, *Evolution and Adaptation* (New York: Macmillan and Co., 1903). Quoted according to the article by G.E. Allen, "Thomas Hunt Morgan and the Problem of Natural Selection," *J. History of Biology,* 1968, *1:* 113-139.

evolutionary process and toward the assumption of the inheritance of acquired characters. Turning to the Russians, we should return to Davitashvili's article, already mentioned in connection with Kovalevsky's evolutionary views. This article was dedicated to a search among Russian paleontologists for statements which Davitashvili could construe to be in support of the principle of inheritance of acquired traits.

Davitashvili prefaced his presentation of the views of Nikolai Ivanovich Andrusov with the assertion that "all the paleontological-geological research of Andrusov . . . is very significant for reevaluating the question of directed mutation and inheritance of acquired traits on the basis of fossil material"[37] What emerges from the excerpts of Andrusov's work cited in Davitashvili's article is that Andrusov explained the evolution of fossil features as "the modification of species under the influence of local conditions."[38] Andrusov felt that a new species, "having adapted to conditions different from those to which the parent species was accustomed, could thrive since it did not confront the old, customary competition in this new region."[39] He spoke of various "species and forms which developed under the influence of life in the benthos," and he spoke of escapees from the periphery of a species' range which, "by adapting to new conditions, are modified in a certain direction."[40] Andrusov wrote of the desalination of the Sarmatian Sea, which he said would surely "obliterate the fauna of the benthos, which was sensitive to abrupt changes, while in the littoral fauna many forms capable of surviving this stress could be found."[41]

These and other places in the papers of Andrusov attest to his Darwinian conception of the evolutionary process. Without explicitly using the concept of natural selection, Andrusov everywhere spoke of the survival or extinction of this or that form in favorable or unfavorable conditions. Therefore Davitashvili's evaluation of Andrusov's views seems completely unfounded, and the following words of that author further exemplify this point: "Andrusov was convinced of the heritability of traits acquired by the organism as the result of interaction with its environment."[42] Where Davitashvili attributed to Andrusov the assertion of a directed mutability as if it were the result of a purposeful reaction to external influences,

[37] Davitashvili (n. 19), p. 75.

[38] Nikolai Ivanovich Andrusov, "Ocherk istorii razvitiia Kaspiiskogo moria i ego obitatelei" ["Outline of the History of the Caspian Sea and its Inhabitants"], *Izv. Russk. geog. ob-va* [*Proceedings of the Russian Geographical Society*], 1889, *24:* 105.

[39] *Ibid.*, p. 107.

[40] Nikolai Ivanovich Andrusov, "O kharaktere i proiskhozhdenii sarmatskoi fauny" ["On the Character and Origin of Sarmatian Fauna"], *Gorn. Zhurn.* [*Mining Journal*], 1891, *1:* 261.

[41] *Ibid.*, p. 262.

[42] Davitashvili (n. 19), p. 81.

Andrusov had actually spoken of directed evolution which, as is well known, is the consequence of natural selection.

The views of Iakovlev which Davitashvili reviewed are indeed close to a Lamarckian's. One might conclude this mainly from the fact that Iakovlev underestimated the role of natural selection. In this spirit Davitashvili emphasized Iakovlev's assertions that change in organisms depends on the conditions of the environment, in particular, mechanical influences. Nowhere, however, in the quotations given by Davitashvili in his article does Iakovlev speak directly of the inheritance of changes brought about by the direct influence of environment.

Davitashvili spoke as a proponent of the inheritance of acquired traits not only in his capacity as an historian of paleontology, but as a paleontologist himself. Striving to substantiate the position that phylogenetic changes are the result of "nurture," that is, the influence of the surrounding environment, Davitashvili was forced to start with the following assumption: "To establish the change-creating action of the environment on the organism on paleontological evidence is, generally speaking, not easy. It is a complicated matter. To do this one must explain not only the path of phylogenetic development of the organism, but the path of the development of the environment, . . . the consecutive changes in this environment."[43] Besides this, Davitashvili mentioned the principal difficulty confronting the paleontologist, given such a goal—namely, his lack of a genuine proof that phylogenetic changes in organisms were the consequence of the direct action of external influences. In view of the fact that such proof does not and cannot exist, Davitashvili modified his argument concerning observations made by paleontologists, including his own. He wrote, "The rapid transformation of the majority of molluscan faunas in one direction in a very short period [their diminution in size during the middle Miocene—L.B.] can be understood only if we assume a powerful direct influence of the altered conditions of life on the nature of the organisms."[44] Despite the obvious insufficiency of such arguments for solving the question of the mechanism of evolutionary changes, Davitashvili wrote at the end of his article, "The study of paleobiological material allows one in many instances to establish with full assurance the concept of an unquestionably directed mutation, evoked and directed by the conditions of life and by their changes."[45]

[43] Leo Shiovich Davitashvili, "Paleobiologiia i problema vospityvaiushchego deistviia sredy na prirodu organizma" ["Paleobiology and the Question of the Cultivating Effect of the Environment on the Nature of the Organism"], *Vestn. Mosk. un-ta* [*Moscow University Herald*], 1949, *no. 10:* 140.

[44] *Ibid.*, p. 144.

[45] *Ibid.*, p. 148.

More recently Davitashvili again expressed similar views concerning the possibility of the inheritance of changes brought about by environmental conditions and fixed in the evolutionary process by natural selection. He also referred to the same unconvincing experimental and paleontological data.[46]

In conclusion, we should emphasize [on the one hand,] that the facts, that is, the uncovered specimens of the paleontologist, cannot serve as evidence either for or against the assumption of the inheritance of acquired characters. On the other hand, the paleontologists's inquiry into that theme has greatly assisted in the clarification of the theoretical side of the question.

[46] Leo Shiovich Davitashvili, *Voprosy metodologii v izuchenii evoliutsii organicheskogo mira* [*Questions of Methodology in the Study of the Evolution of the Organic World*] (Tbilisi: 1968), 214 pp. Davitashvili, "Deficiencies of the Synthetic Theory of Evolution," *Evolution*, 1969, *23:* 513-516.

CHAPTER 7

Discussion of the Hypothesis of Inheritance of Acquired Characters at the End of the Nineteenth Century

One can already find grounds for doubting the inheritance of environmentally induced traits in the observations of Alexis Jordan. His work belongs to the middle of the last century but was published only much later.[1] Studying the multitude (approximately 300) of varieties of spring whitlow grass, *Erophila* (*Draba*) *verna* [of the mustard family], Jordan tried to clarify experimentally whether these were only varieties or were actually independent species. He regarded as independent species those forms that retained their inherited features over several generations when raised in a soil unusual for them.

The experiments which Carl Nägeli conducted twenty years later were much more convincing.[2] Nägeli transplanted alpine plants to a botanical garden in Munich and demonstrated through such experiments that many of the species studied changed to the point of being unrecognizable, e.g., low-growing alpine forms of hawkweed became large, branched, and bore many flowers. If such plants or their descendents were transplanted to a rocky soil the new traits disappeared completely and the plants returned to their original alpine form. The complete return was observed even when the alpine plants had been cultivated in rich garden soil over many generations.

The Dorpat zoologist, Georg Seidlitz, effectively contrasted the Lamarckian theory of evolution through direct adaptation, to which Haeckel's views were very close, with the Darwinian theory of evolution via natural selection. His views appeared in an unjustly forgotten book published first in Dorpat and later, in an expanded version, in Leipzig.[3]

[1] Alexis Jordan, *Remarques sur le fait de l'existence en société à l'état sauvage des espèces végétables affinées et sur d'autres faits relatifs à la question de l'espèce* (Lyon: 1873).

[2] Carl Wilhelm von Nägeli, Entstehung und Begriff der naturhistorischen Art," *Sitzber. bayrisch. Akad. Wiss.*, 1865, *18*. Works of Jordan and Nägeli are quoted according to August Weismann, *Die Bedeutung der sexueller Fortpflanzung für die Selektionstheorie* (Jena: 1886).

[3] Georg Seidlitz, *Die Darwin'sche Theorie. Elf Vorlesungen über die Entstehung der Tiere und Pflanzen durch Naturzüchtung* (Dorpat: 1871. 2nd ed.; Leipzig: 1875). Born in 1840 Seidlitz was a native of St. Petersburg. His book, according to S.L. Sobol', represented one of

(*contd.*)

Georg Seidlitz
(1840-1917)

Seidlitz proposed a sharp distinction between innate and acquired traits. In his opinion, the former were, as a rule, inherited, while the latter were usually not transmitted to progeny. In discussing this question, Seidlitz treated particularly those cases drawn on by Darwin as demonstrating the inheritance of acquired traits. For example, Heinrich Georg Bronn told of a case where a cow which had lost one horn due to infection gave birth to three calves with the same defect; Blumenbach referred to sons who inherited the injury to a finger which their father had suffered; Adam Sedgwick cited a story of a soldier, blinded in one eye fifteen years before marriage, whose sons exhibited microopthalmia on the same side. Not questioning the credibility of these communications, Seidlitz confined

the best courses in its day on Darwinism. This course, however, was not offered for long. According to E.E. Martinson, historian at Tartus University, "the attempt by Docent Seidlitz to lecture on Darwinism was suppressed in the 1870s." For Sobol's comment see the footnote in Charles Darwin, "Vospominaniia" [*Autobiography*], *Soch.* [*Works*], 1959, *9:* 436. For Martinson's remark see "Istoricheskie sviazi Tartuskogo universiteta s russkoi naukoi" ["Historical Connections of Tartus University with Russian Science"] (Talin: 1951), p. 67. Concerning the scientific activity of Georg Seidlitz, see L.la. Blacher, "Georg Zeidlits i ego kurs Darvinizma v Derptskom universitete" ["Georg Seidlitz and His Course on Darwinism at Dorpat University"], in the collection *Iz istorii biologii* [*From the History of Biology*], 3rd ed. (in print).

himself to the observation that such examples of the inheritance of an injury were encountered very rarely and should be regarded as exceptions. By contrast, the majority of instances of intentionally inflicted or accidental injuries were not inherited. Addressing the possibility of individual variations arising under the influence of climate, diet, or use or disuse of individual organs, Seidlitz noted that despite the widespread opinion favoring the inheritability of such changes he did not find transmission rigorously proven in even one instance, and therefore its occurrence remained very doubtful. Regarding examples of "transformation" of breeds of horses and dogs upon migration to new locales, Seidlitz wrote that "in not one case was it shown what part was played in this change in offspring by the inheritance of traits received from the parents, and what significance could be attributed to the external conditions (e.g., changed diet) under the influence of which the parents were changed."[3a]

Seidlitz was sure that the appearance in children of individual traits which diverged from those of their parents depended not on acquired but on inherent changes. In new climatic conditions these came under the influence of natural selection which proceeded in a different direction than before so that the original form was eliminated. According to Seidlitz, there was no proof that individual modifications, caused by use or disuse of organs, were inherited, despite the fact that such inheritance should have been easy to establish. After all, intensified development of organs due to their use and underdevelopment due to their disuse were among the most common of phenomena. Seidlitz supported his opinion by referring to the thickening of skin on palms and soles. Darwin had referred to this phenomenon, and it was often construed as a case of the inheritance of an acquired trait. Seidlitz would have accepted as proof of this interpretation the demonstration that one brother, having walked barefooted from youth, bore children with thicker skin on their soles than the children of his brother who always wore shoes. There was not such proof available, however, and therefore the described changes in thickness of skin should be attributed to natural selection. Similarly, the origin of knee joint callouses in camels and certain breeds of sheep ought to have been explained by the natural selection of inherent changes without assuming the inheritance of acquired traits.

Seidlitz did admit the possibility of the inheritance of acquired changes in habits and instincts, though later he questioned the possibility. Having cited Darwin's unconvincing examples of the reproduction in children of behavioral traits of their parents, Seidlitz went on to treat habits in animals. Habits displayed over many generations could, according to Seidlitz, be regarded as inherited from the progenitors in which they first

[3a] Seidlitz, *ibid.*, p. 135. This and further references are based on the second German edition. [English translations are taken from the Russian.]

arose as acquired traits. He did not, however, exclude the alternative explanation, namely, that an inheritable inclination for the corresponding habit might exist in a latent form in the embryo.

Seidlitz argued in detail the importance of recognizing the presence of heritable traits in a latent state. "Before the trait is revealed at its appropriate time, one must not speak of its absence. Such a trait should be called latent, i.e., not yet developed, though capable of development."[4] Examples of such latent traits included the rudiments of teeth in newborn children, the anlagen of the urogenital organs in the form of the Wolffian body, and latent traits of the adult crustacean in its larva, a nauplius or zoea. In such a latent form all the traits of the future organism, without exception, existed in the egg. Similarly latent were the milk-producing capacity transmitted from a bull to its daughters, traits of the drone developing from its parthenogenic egg, traits of the medusa hidden in the planular forager but appearing by budding in the developing medusa. All instances of atavism belonged to this category. In Seidlitz's thinking, these examples of the inheritance of latent traits supported the idea that in respect also to habits we should speak not of their appearance in the adult individual as acquired traits and their subsequent transmission to offspring, but of the inheritance of inborn latent propensities which favor the development of the corresponding form of behavior.

According to Seidlitz, inherent properties were much more important for evolution than acquired ones. In support of this assertion and likewise in support of a belief in evolution via natural selection rather than direct adaptation, he mentioned the following considerations: if in the process of evolution acquired traits had greater significance, as Haeckel assumed (Seidlitz referred to chapter 19 of the second volume of the *Generelle Morphologie*), then evolution would proceed much faster in nature, namely, at the same rate as form is changed in domestic breeding. The progeny of an organism which had been subjected to a new influence would change to the same degree and in the same direction over several generations if they remained in the same change-producing conditions as their progenitor. Also, if the progeny were subjected to novel environments, they would yield an equal number of new varieties. In either case, none of the individuals would have an advantage over the others, and no competition, the basis of natural selection, would occur among them.

Seidlitz pointed out that one may speak of direct adaptation only in relation to traits under the immediate influence of external factors or of use or disuse of organs. The concept of direct adaptation was completely inapplicable to instances of protective coloration, mimicry, and passive defensive adaptation, as well as to traits subject to the action of sexual selection.

[4] *Ibid.*, p. 139.

The concept of direct adaptation was also inapplicable to eggs after they had been laid and no longer changed. All adaptations of eggs to the conditions of the surrounding environment (e.g., color and make-up of the shell) have great significance for the survival of the embryos developing from the eggs. These adaptations could only be explained by natural selection, acting upon the possible differences in the egg-forming apparatus of the mother, on which differences in eggs also depended.

Seidlitz considered it especially important to analyze the origin of changes during the process of evolution which gave rise to the various forms in a colony of social insects, in particular, to their specialized instincts. Features of behavior, e.g., the instincts of worker bees, could not have arisen by way of exercise as an adaptive response to factors of the environment and then have been fixed in their offspring since the possessors of these instincts do not reproduce and cannot transmit their instincts to succeeding generations. Besides, the development of this behavior was fully explainable by natural selection acting on the reproductive individuals of the colony. After all, progenitors of a colony would have a selective advantage if they possessed the genetic constitution leading to the expression of that behavior in worker bees which was useful to the entire colony. This proposal was developed in greater detail in a postscript. Seidlitz wrote, "Bees serve as an excellent example of the fact that latent traits can become more intense and can become fixed through natural selection. In the queen bee and drones, worker bee instincts useful to the bee colony remain in the latent state and are not influenced by use or disuse, i.e., they develop other than by 'direct adaptation' (Haeckel). Conversely, worker bees, in whom these instincts might develop via direct adaptation, transmit nothing by inheritance. The development of the corresponding behaviorial traits may depend on the fact that the queen bee transmits latent instincts by inheritance to her fertile daughters, . . . thereby entering into a passive competition with the queens of other colonies. . . . Here we have excellent evidence in support of the theory of natural selection and against the direct accommodation urged by the Lamarckians. We have, as well, support of the idea that for evolution inherent individual differences are more important than acquired ones."[5]

In 1876 Seidlitz returned to a criticism of the concept of evolution based on direct adaptation and its inheritance in another book, *Contributions to the Theory of Evolution.* He devoted the second part of this work to a polemic against Karl Ernst von Baer, who in the same year had spoken out in opposition to Darwin's theory.[6]

[5] *Ibid.*, p. 264.

[6] Karl Ernst von Baer, "Über Darwin's Lehre." *Reden gehalten in wissenschaftlichen Versammlungen und kleinere Aufsätze vermischten Inhalts,* 3 vols. (St. Petersburg: H. Schmitzdorff, 1864–1876), III, 235–480.

An important feature of this second work consisted of Seidlitz's observation that von Baer's objections should properly be addressed, not to Darwin, but to his predecessors, Lamarck and Geoffroy Saint-Hilaire, and especially to Haeckel, who confounded the evolutionary views of Lamarck and Darwin. "When Darwin speaks of active or direct 'adaptation,'" wrote Seidlitz, "he strongly emphasizes the idea that even though it is unquestionably strongly reflected in the individual, it probably plays a completely subordinate role in the transformation of species.... Here precisely is found the most important difference between the theory of selection and the Lamarck-Geoffroy theory of accommodation. Certain contemporary investigators, for instance Haeckel, however, assign greater significance to the latter theory, and they therefore do not speak in harmony with the theory of selection but contradict it."[7]

To create a clear understanding of the principle difference between doctrines of evolution via direct adaptation and those via natural selection, Seidlitz concentrated on an analysis of the concept "adaptation." He noted that although Darwin did not give that term its original definition, it was easy to distinguish between the Darwinian and Lamarckian use of "adaptation." While in Lamarck's doctrine adaptation was regarded as an active and satisfactory response to the influence of surrounding conditions, Darwin, in *The Origin of Species* and other works, used the word "adaptation" as a technical term, in lieu of the lengthy phrase "survival of the most adapted in the struggle for existence."

In the classification of phenomena of adaptation contained in Haeckel's *Generelle Morphologie* one finds many markedly artificial constructs. Among them are "general," "accumulating," and "correlative" adaptations, which Haeckel assigns to the category of "direct, or active, adaptations," that is, those adaptations which are based on acquired individual changes and which do not involve natural selection. Haeckel viewed all these forms of adaptation in the spirit of the Lamarckian theory, and he left out of his classification adaptation in the Darwinian sense, that is, that arising via natural selection. Seidlitz correctly noted that this difference was evident from the fact that Haeckel "contrasted heredity and adaptation as 'antagonists,' and thus obviously did not have in mind adaptation through natural selection, which turns out to be the necessary consequence of the inheritance of useful variations."[8]

One of the first to express doubts of the heritability of acquired traits on the basis of theoretical reasoning and experimental data was Francis Galton. We spoke earlier (chapter 4) of Galton's experiments which refuted

[7] Georg Seidlitz, *Beiträge zur Descendenz-Theorie.* (Leipzig: Wilhelm Engelmann, 1876). [See particularly pt. II "Baer und die Darwinsche Theorie," quotation appears on pp. 66-67.]

[8] *Ibid.*, p. 124.

Darwin's theory of pangenesis. In 1875 Galton wrote an article, "Theory of heredity," which presented general considerations on the issue of the inheritance of acquired traits. To the question do somatic cells at all affect the sex elements, he answered, "We may be confident that at the most they do so in a very faint degree; in other words, that acquired modifications are barely, if at all, *inherited,* in the correct sense of the word."[9]

When August Weismann first declared himself a decided supporter of Darwin's theory, his statement on the general problems of evolution contained no objection to the inheritance of acquired traits.[10] At that time Weismann defined variability as the consequence of the influence of various external factors on the direction of development, that direction being conditioned by heredity. He thus thought that, in addition to heredity, external influences have a role in the evolutionary process and that those influences act in two ways: "first, as a force which modifies heredity and produces individual peculiarities, and second, to a certain extent as a regulator of arisen variations in the form of natural selection."[11]

Much later, while engaged in polemics with Herbert Spencer, Weismann recalled this stand in his work of 1868. "I myself, 25 years ago, still adhered to the view that, besides the primary variation and its accumulation and ordering by natural selection a not insignificant role was played by the inherited influences of use and disuse."[12]

The year 1883 must be considered a decisive moment in the discussion of the problem of inheritance of acquired traits. At that time, upon assuming the position of prorector of the University of Freiburg, Weismann gave a lecture, "On heredity." The essay was printed the same year and republished in 1892. As Weismann wrote in the foreword to the second edition of this lecture, he did not discuss the entire problem of heredity, but only those questions which were joined under the topic of inheritance of acquired traits. Weismann pointed out, first of all, "the difficulty, or the impossibility of rendering the transmission of acquired characters intelligible by an appeal to any known forces," although these difficulties still

[9] Francis Galton, "A Theory of Heredity," *J. Anthropol. Inst.*, 1875, *5:* 346.

[10] On the following pages the views of August Weismann concerning the problem of the inheritance of acquired characters and associated questions are rather extensively presented. This was deemed necessary because Soviet readers interested in theoretical questions of biology are for the most part familiar only with Weismann's *Lectures On the Theory of Evolution,* which were published in Russian at the beginning of the century.

[11] August Weismann, "Über die Berechtigung der Darwinschen Theorie. Ein akademischer Vortrag gehalten am 8 Juli 1868 in der Aula der Universität zu Freiburg." (Leipzig: 1868.) Quoted from the book: Ernst Gaupp, *August Weismann: Sein Leben und sein Werk* (Jena: Gustav Fischer, 1917), p. 65.

[12] August Weismann, *Die Allmacht der Naturzüchtung: Eine Erwiderung an Herbert Spencer* (Jena: Gustav Fischer, 1893), pp. 42-43. ["The All-sufficiency of Natural Selection," *Contemp. Rev.* 1893, *64:* 309-338, 596-610.]

did not allow one "to cast doubts upon the very existence of such a form of heredity." The widespread belief in the possibility of inheritance of acquired traits depended, in Weismann's opinion, first, on the fact that "observations have been recorded which appear to prove the existence of such transmission," and second, "it has seemed impossible to do without the supposition of the transmission of acquired characters, because it has always played such an important part in the explanation of the transformation of species."[13]

Eduard Pflüger
(1829-1910)

Both Weismann and the physiologist-embryologist Eduard Pflüger simultaneously reckoned that a rigorous proof of the inheritance of acquired traits did not exist and that it had not been demonstrated that the inheritance of acquired traits was a necessary condition for transformation in the organic world. In particular, Pflüger wrote, "I closely familiarized myself with all the facts which were cited in support of the inheritance of acquired traits, namely, those which do not have their basis in the original organization proper of the egg and sperm which gave the individual its

[13] August Weismann, "Über die Vererbung," (Jena: Gustav Fischer, 1883) ["On Heredity" in *Essays upon Heredity*, ed. Edward B. Poulton, Selmar Schönland, and Arthur Shipley, 2 vols. (Oxford: The Clarendon Press, 1891-2), I, 81.]

beginning, but were acquired later through purely random external influences on the organism. Not one of these facts proved the inheritance of acquired traits."[14]

In 1883, Weismann also reckoned that "the inheritability of acquired changes is completely unsubstantiated either by simple observation or by experiment. The literature contains a sufficient number of instances which are claimed to prove that injuries—the loss of a finger, a scar, a wound received earlier, etc.—are inherited by the offspring, but in all of these instances the preceding history of like events is obscure, and therefore scientific criticism is impossible."[15]

In the work discussed, due to a lack of precisely designed experiments, Weismann was limited to theoretical considerations. Besides, as he noted, there was a widely held conviction that a large number of phenomena could only be understood in terms of the inheritance of acquired traits (e.g., use and disuse of organs, direct influence of climate, the origin of instincts regarded as "habits become hereditary," and the like). At first glance, as Weismann remarked, it seemed irrational to try to get along without that hypothesis. "I will now," he continued, "attempt to prove that even these cases, so far as they depend upon clear and indubitable facts, do not force us to accept the supposition of the transmission of acquired characters."[16] In his arguments Weismann strove to show that phenomena taken to be the result of the inheritance of acquired traits were also quite adequately explained in terms of the activity of natural selection. He wrote, "we may urge that whenever, in the course of nature, an organ becomes stronger by exercise, it must possess a certain degree of importance for the life of the individual, and when this is the case it becomes subject to improvement by natural selection, for only those individuals which possess the organ in its most perfect form will be able to survive. . . . The increase of an organ in the course of generations does not depend upon the summation of the exercise taken during single lives, but upon the summation of more favourable predispositions in the germs. . . . We cannot by excessive feeding make a giant out of the germ destined to form a dwarf; we cannot, by means of exercise, transform the muscles of an individual destined to be feeble into those of a Hercules, or the brain of a predestined fool into that of a Leibnitz or a Kant, by means of much thinking."[17] In this connection, Weismann referred to examples borrowed from Darwin of the advantage of atrophic changes for various animals, e.g., the underdevelopment of such

[14] Eduard Pflüger, "Uber den Einfluss der Schwerkraft auf die Teilung der Zellen and au die Entwicklung des Embryo," *Arch. Physiol.*, 1883, *32:* 68.

[15] Weismann (n. 13), pp. 81-82. [References follow the English edition.]

[16] *Ibid.*, p. 83.

[17] *Ibid.*, pp. 84-85.

organs as wings in insular insects, eyes in underground mammals, and legs in snakes. In particular, despite the fact that the eyes of blind cave fish and amphibians are covered by skin, they may be rather well developed. Weismann considered this fact incompatible with traditional views ascribing underdevelopment of eyes to disuse, for if this were so, the organ should have completely disappeared.

Although during this period of his research Weismann noted that the essence of such phenomena was so little investigated that solving the question of the original causes would prove difficult, he still allowed that changes evoked by the immediate influence of altered external conditions were inheritable. He reckoned, for example, that climatic influences could act directly to modify the sex cells. Enhanced or reduced nourishment, leading to the more luxuriant growth of this or that plant, caused the formation of correspondingly larger or smaller seeds, which in turn was reflected in the development of plants of the next generation. But Weismann did not regard these examples as arguments in support of the inheritance of acquired traits, since he thought changes in the character of growth and development were the consequence of a direct quantitative influence acting simultaneously on the vegetative and generative elements.

In one of his early works,[18] Weismann saw no possibility of explaining the appearance of climatic varieties in butterflies other than by the inheritance of changes acquired passively, that is, under the direct influence of climate. In 1892 he continued to hold to his former opinion in regard to this example but he added that "innumerable cases exist in which we can certainly exclude all assistance from the transmission of acquired characters.... In all such cases we have no explanation except the operation of natural selection, and if we cannot accept this, we may as well abandon any attempt at a natural explanation."[19]

According to Weismann, quantitative changes were the prime material for selection, and each of the traits which varied in magnitude could prove useful to a certain degree and, in accordance with conditions, would be progressively magnified or diminished. Changes in the sex cells, according to Weismann, comprised the basic source of variation, which then came under the action of natural selection. External influences acting on developing individuals determined the appearance of individual changes, the amplitude of these changes being limited by inherited possibilities. As such changes, transmitted from generation to generation, led to quantitative variations of inherited properties, the question of the origin of these

[18] August Weismann, *Studien zur Deszendenztheorie. I. Über den Saison-Dimorphismus der Schmetterlinge* (Leipzig: 1875).

[19] Weismann (n. 13), pp. 101–102.

variations was solved. Weismann wrote, "I believe however that they [variations] can be referred to the various external influences to which the germ is exposed before the commencement of embryonic development."[20]

Already in the first edition of his earlier work [1883], Weismann had formulated the fundamental elements of the theory of the germ-plasm which he later developed more fully. It amounted to: first, the idea that the germ-plasm, whose presence in sex cells was necessary for the inheritance of inherent traits, was transmitted without interruption from generation to generation and, second, the idea that the germ-plasm and somatoplasm change. Change in the germ-plasm, however, should precede the corresponding transmitable changes in the somatoplasm. Weismann proposed to distinguish the continuity of individuals from the continuity of a species, changes in the latter of which constituted evolution. When individuals replaced one another, the germ-plasm remained one and the same, whereas when one species was transformed into another, the germ-plasm underwent changes.

Weismann developed to its logical extension the idea of the continuity of the germ-plasm in treatises published two and three years later, "The continuity of the germ-plasm as the foundation of a theory of heredity" (1885) and "The significance of sexual reproduction in the theory of natural selection" (1886), as well as in the article "On the question of the inheritance of acquired traits" (1886).

The idea of the continuity of the germ-plasm proceeded from the immediately observable. The connection between successive generations was established by means of sex cells. Since the male gamete consisted practically of only a nucleus and since, in any case, upon fertilization of the egg only the nuclear part of the sperm penetrated, as Oscar Hertwig showed (1875), it was natural to conclude that deposits of inherited properties were localized precisely in the nucleus. Data from the early isolation of sex cells, in particular, those observations on the development of insects carried out by Weismann (1864) and confirmed by Ilya Mechnikov (1866), served as the basis for the next conclusion. In the process of formation of the embryo, part of the germ-plasm of the fertilized egg, according to Weismann's hypothesis, remained unused in the formation of organs and was part of the future sex cells of the new organism. Using a comparison proposed earlier by Galton, Weismann wrote that the germ-plasm is like a "long creeping rootstock from which plants arise at intervals, these latter representing the individuals of successive generations." From this conception, as Weismann thought, there followed the conclusion about the heritability of acquired traits. "If the germ-plasm is not formed anew in each individual, but derived from that which preceded it, its structure, and

[20] *Ibid.*, p. 105.

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above all its molecular constitution, cannot depend upon the individual. . . . the tendencies of heredity, of which the germ-plasm is the bearer, depend upon this very molecular structure, and hence only those characters can be transmitted through successive generations which have been previously inherited, viz. those characters which were potentially contained in the germ-plasm. It also follows that those other characters which have been acquired by the influence of special external conditions, during the lifetime of the parent, cannot be transmitted at all."[21]

Weismann proposed to distinguish clearly nonheritable individual changes from heritable changes. From identical embryos developing in different conditions, unlike individuals were formed. Their variations, depending on nourishment and use and disuse of organs, were not inherited, so Weismann considered these differences transient. To illustrate this thought, he referred to the fact that children of a musician do not inherit the art of playing from their father. In order to become musicians, they must study intensely just as their father did. Likewise, for a child to master speech, he must be taught to speak although a long line of his predecessors

[21] Weismann (n. 2), p. 20. [Quotation follows the English trans. "The Significance of Sexual Reproduction in the Theory of Natural Selection" found in *Essays* (n. 13), p. 272.]

exercised their organs of speech. What then is the nature of transmitted changes if it was recognized that the results of learning, as well as other acquired habits, were not inherited? Weismann answered this question: "In the first place it may be argued that external influences may not only act on the mature individual, or during its development, but that they may also act at a still earlier period upon the germ-cell from which it arises. It may be imagined that such influences of different kinds might produce corresponding minute alterations in the molecular structure of the germ-plasm, and as the latter is, according to our supposition, transmitted from one generation to another, it follows that such changes would be hereditary."[22]

We should pay special attention to this excerpt, since it contains the idea Weismann repeated many times, that the germ-plasm can change under the influence of external conditions.[23] It is important to remember this idea of Weismann, especially since it was forgotten by all who, in the polemic with Weismann, referred only to his insistence on the durability of germ-plasm in the face of influences from outside (on the part of the soma and surrounding environment). According to Weismann, heritable changes, which depended on external influences, were combined during amphimixis, that is, with the mixture of the germ-plasms of father and mother in sexual reproduction.

The publication by the Tübingen zoologist Theodor Eimer of his book, *Organic Evolution as the Result of the Inheritance of Acquired Characters,*[24] belongs to the period of Weismann's activity just examined. Arbitrarily comparing the origin of organic forms to crystallization, Eimer viewed the world of living beings as a single whole, growing and changing under the influence of external influences. According to Eimer, these changes occurred because acquired traits became hereditary. In characterizing Eimer's conception, Nikolai Aleksandrovich Kholodkovskii justly commented that "Eimer merely repeated the old teaching of Lamarck, theoretically adding almost nothing to it. . . . With regard to the special question of the transmission by heredity of acquired features, Eimer cited a whole list of examples in proof of that transmission. But these examples were partly old, partly inconclusive, and all explainable from the viewpoint of Weismann's theory."[25] In Kholodkovskii's opinion, Eimer's theory

[22] *Ibid.*, p. 277.

[23] See, for example, references to corresponding passages in Weismann's book, *Das Keimplasma: Eine Theorie der Vererbung* (Jena: Gustav Fischer, 1892), pp. 102-104.

[24] Gustav Heinrich Theodor Eimer, *Die Entstehung der Arten auf Grund von Vererben erworbener Eigenschaften nach den Gesetzen organischen Wachsens, Ein Beitrag zur einheitlichen Auffassung der Lebewelt,* 3 vols. (Jena: Gustav Fischer, 1888-1901), I, 46.

[25] Nikolai Aleksandrovich Kholodkovskii, "Staryi i novyi lamarkizm" ["The Old and New Lamarckism"], *Biologicheskie ocherki* [*Biological Profiles*] (1932), p. 40.

seemed especially weak and naive in comparison with Nägeli's theory of idioplasm and Weismann's theory of germ-plasm, the harmony and completeness of which (especially of the latter) were undeniable.

In order to clarify as much as possible the variety of changes in the organism, Weismann introduced the distinction between somatogenic and blastogenic traits. He considered somatogenic traits those which arose in the response of the whole body (soma) or of individual parts to external influences. One might speak of the inheritance of acquired traits in the original sense of the expression only in the situation where a somatic trait appeared in the course of the organism's individual life and when the changed soma itself, rather than the immediate influence which evoked that change, induced a change in the germ-plasm that in turn produced the same somatogenic change in the following generation. Carl Detto later called this hypothetical process somatic induction. According to Weismann, the only source of [new] blastogenic traits were the newly arising changes in the germ-plasm. These would reach the following generation through the sex cells of the parent and develop into altered somatic traits. Weismann clarified the difference between somatogenic and blastogenic traits in the following example: "If a person has a severed finger, his four-fingeredness is a somatogenic or acquired trait; but if a child is born with six fingers, then his six-fingeredness is the result of a special trait of the germinal substance and is thus a 'blastogenic' trait."[26]

As is well known, the possibility of inheritance of somatogenic traits was allowed by many authors in the seventies and eighties of the past century, among them Darwin and especially Haeckel (see chapters 4 and 5). Examples of a hornless calf born to a cow which had accidentally lost its horn, of tailless kittens and puppies born to mothers with severed tails, and other analogous examples were cited in great numbers in agricultural and popular literature. Following the example of Wilhelm His, who in his time ridiculed such stories, Weismann subjected communications of this kind to detailed criticism; he showed that some of the instances could not even be discussed, due to the inexactness and unreliability of the facts themselves, and that others invited an altogether different and well-founded explanation. In particular, concerning the case of tailless cats, Weismann was aware that the trait might not at all be due to injury to the tail of the forebears. On the Isle of Manx and in Japan there have long been breeds of tailless cats. The situation is the same with sheep. On the one hand, the cutting off of the tail in some breeds does not lead to a transmission of the inflicted defect, while on the other hand, there are races in which the absence of the tail is an inherent trait. Rudimentariness of the small toe in man is not at all the result of the inheritance of the influence of pressure by shoes, since the small toe is also rudimentary among people who over many generations have walked barefoot. The results of intentional injury to man, done for ritual or "esthetic" reasons—e.g., scarification, piercing of ears, lips, nose, extraction of teeth, and deformation of feet and skull—are not inherited, as is well known. It would seem that this conclusion needed no confirmation by special experiments.

[26] August Weismann, "Über die Hypothese einer Vererbung von Verletzungen," S. 8-9, footnote in *Aufsätze über Vererbung und verwandte Biologische Frage* (Jena: Gustav Fischer, 1892) p. 513n. [This footnote does not appear in the English version printed in *Essays* no. 13.]

Weismann, nevertheless, deemed it necessary to set up such experiments. Upon reviewing Weismann's arguments disputing the contemporary popular belief in the transmission of mechanical injuries, Osborn likened them to Don Quixote's jousting with windmills.[27] Instances of the underdevelopment of the tail among cats and dogs, regardless of whether the parents' tails were cut off or not, are not rare. Weismann therefore used animals in which such a spontaneous shortening of the tail was not known to occur, namely, white mice and rats. He first reported the results of his experiments of amputating the tails in five generations of mice, in a lecture at the Congress of Naturalists and Physicians in Cologne, 20 September 1888. At the time of the lecture, he had examined, in all, 849 progeny of experimental mice. The tail amputations among progenitors had not had any influence on the size of tails in the progeny. Tail length among the newborn of control mice varied within very narrow limits—from 10.5 to 12.0 mm. Not one of the baby mice of the experimental group had a tail shorter than 10.5 mm.

Realizing that his experiment did not establish once and for all the impossibility of inheritance of an injury, Weismann foresaw the objection that the transmission of an injury needs a greater number of generations experiencing identical injuries. To defend his interpretation, Weismann pointed out that the majority of cases which served as arguments in support of inheritance of an injury were one-time injuries to one of the parents and that investigators supposed that the results of such injuries were inherited even in the immediately following generation. Consequently, Weismann's negative results, in an experiment in which both parents were injured over several generations, should be considered significantly more conclusive.[28] In 1892 Weismann mentioned the continuation of his experiment on mice in his book *The Germ-plasm,* by which time the number of generations examined had reached nineteen. He was now able

[27] Henry Fairfield Osborn, *From the Greeks to Darwin. An Outline of the Development of the Evolution Idea* (New York: London: 1929), p. 193.

[28] Weismann (n. 26), p. 21 and Weismann (n. 23), p. 520.

to refer to the corroboration of his results in experiments by J. Ritzema-Bos[29] and Julius Rosenthal.[30] The final results of his experiment were included in Weismann's *Lectures on Evolutionary Theory*.[31] In the twenty-two generations of mice that underwent tail amputation not one of the 1592 offspring examined showed the absence or a foreshortening of the tail.

This study has been quoted many times, frequently in an ironic spirit. As Weismann's biographer Ernst Gaupp wrote, several of the authors who cited this work, such as Osborn, expressed perplexity over why Weismann spent so much time and effort in proof of a completely indisputable truth. If we turn to the literature of that period, however, it is not difficult to convince ourselves that the question was still very much a moot point, and if it was viewed differently by the time Gaupp wrote about it, science is indebted to Weismann for this.[32]

In essence, Weismann's most important contribution, which Gaupp failed to point out, was not the definitive resolution of the question of the transmission of mechanical injuries but a new methodological approach to the discussion of the whole problem of inheritance of acquired traits. After Weismann's investigation in spite of all its naiveté from a modern viewpoint, it became perfectly clear that *a priori* argumentation, by whatever "higher arguments," was completely inadequate to answer the question of the transmission of any acquired trait. The natural method by which to silence the disputing parties was the experimental method. It was only after Weismann's experiment amputating mouse tails, conducted incidently, without sufficiently strict observance of the methods of investigation, that investigators realized that strict criteria for such experiments should be worked out. These included determining the genetic purity of the original experimental material and providing precise quantitative data of traits in terms of size and number.

The results of Weismann's experiment could not, of course, convince those of his opponents who insisted *a priori* that the inheritance of acquired traits was a necessary condition of evolution. The pet argument of these authors was to claim that evolutionary changes were so protracted that they could not be reproduced. Wilhelm Haacke in his lengthy polemical essay, *Form and Heredity*, cited facts which, in his opinion, confirmed the inheritance of acquired traits. "Where we find any organ which by virtue of its activity has significance for the organism, we have a matter of acquisition which is fixed by heredity over the course of generations and is preserved and perfected by continuous use. . . . I am perfectly aware that many naturalists demand experimental proof of such a contention. I answer that the entire world of organisms is the result of a huge experiment relating to heredity, which was set up by nature. To demand that nature set up her experiment so that it could easily be repeated by a doubting armchair scientist, seems to me to go beyond reason. What nature required probably millions of years to accomplish, they hope to carry out at the Freiburg Zoological Institute during the directorship of one single professor-preformationist, and since they don't succeed, they simply reject the inheritance of acquired traits."[33]

[29] J. Ritzema-Bos, "Zur Frage der Vererbung von Traumatismen," *Biol. Zbl.*, 1891, *11:* 734–36.

[30] Julius Rosenthal, "Zusatz zur Mitteilung des Herrn Ritzema Bos," *Biol. Zbl.*, 1891, *11:* 736.

[31] August Weismann, *Vortäge über Deszendenztheorie*, 2 vols. (3rd ed; Jena: Gustav Fischer, 1913), II, 70.

[32] Gaupp (n. 11), pp. 86–87.

In another passage from the same book Haacke wrote, "What can laboratory experiments on the inheritance of injuries tell us at all, even if someone conducts them over the course of his entire life? What does a human lifetime mean in comparison with the time the histories of development of organisms took for their experiments? And what does a pair of cages and some white mice in some room of a zoological institute count for in comparison with the great Laboratory of Nature? We must turn to the experimentor's art of nature if we want to get an answer to the question of whether injuries are inherited, and nature shows us that the inheritance of injuries indeed takes place, if the corresponding experiment is conducted suitably over a sufficiently long time in every generation."[34] As examples of such natural experiments which proved, in his opinion, the inheritance of acquired injuries, Haacke noted the disappearance of feathers around the beaks of rooks, which he explained by the fact that rooks constantly poke their beaks into the ground in attaining their food, and the disappearance of fur on the sciatic callouses of monkies and on the soles and other surfaces of the body of mammals subject to friction. Haacke especially emphasized the first example, although it in no way differed markedly from others recalled countless times from the days of Lamarck. All such phenomena were quite familiar to Weismann, who validly attributed the results of such "natural experiments" to the operation of natural selection.

Haacke attempted to base his conviction of the inheritance of acquired traits on completely arbitrary, far-fetched ideas about the structure of the protoplasm which, according to his hypothesis, was comprised of particles (gemmae) in the form of rhombic prisms, either tightly or loosely joined to one another. The influence of external conditions apparently led to the displacement of gemmae, and this displacement, originating in any part of the body, was somehow transmitted to all the cells of the body, among them

[33] Wilhelm Haake, *Gestaltung und Vererbung: Eine Entwicklungamechanik der Organismen* (Leipzig: 1893), S. 107–108.

[34] *Ibid.*, p. 297. [Translation taken from the Russian.]

the sex cells, guaranteeing adequate inheritance of the acquired local change. It is completely incomprehensible how in the 1890s, when histology and cytology had already accomplished significant advances, one could seriously publish such fantasies as Haacke's hypothesis.

Concerning the question of inheritance of functional changes, Weismann noted the generally accepted fact that muscles as well as memory and other functions are strengthened through exercise. Weismann's predecessors, failing to think through the matter, assumed that adaptations of organs to their function or of the organism as a whole to conditions of its existence should be explained as the transmission to successive generations of the results of use of an organ or of individual adaptations. It seemed even more obvious that the underdevelopment of unused organs was the direct consequence of their disuse.

"I myself was of that opinion for many years," wrote Weismann, "and only over the last five years did I gradually come to the conviction that this supposition was incorrect, that inheritance of the results of use or disuse was impossible, and that we therefore must seek another explanation for the corresponding phenomena."[35] Weismann drew attention to the fact that existing references in the literature to inheritance of the results of use or disuse of organs did not contain factual evidence. The use or lack of use of organs exerted influence only on that individual which carried on, to a greater or lesser extent, the corresponding function. In contrast, the cases which seemed to show transmission to progeny of the results of functional changes could be explained by the natural selection of favorable changes which, depending on circumstances, might be a strengthened or weakened state of the organ.

In a more thorough manner than in his previously mentioned shorter works, Weismann considered the problem of inheritance of acquired traits in *The Germ-plasm.* A special chapter entitled "Supposed Transmission of Acquired Traits," concentrates specifically on this problem. Weismann repeated here his distinction between "somatogenic" and "blastogenic" traits and his belief that "every permanent variation proceeds from the germ in which it must be represented by a modification of the primary constituents."[36]

Weismann prefaced his examination of the facts confirming or refuting the hypothesis of inheritance of acquired traits with a special section entitled "Difficulties in the way of a theoretical basis for this assumption." Here Weismann offered the opinion that the transmission of somatogenic

[35] August Weismann, "Zur Frage nach der Vererbung erworbener Eigenschaften," *Biol. Zbl.*, 1886, *6:* 42.

[36] Weismann, *Keimplasma* (n. 23), p. 514. [All translation taken from the English, *The Germ-Plasm. A Theory of Heredity*, trans., W. Newton Parker and Harriet Rönnfeldt (New York: Charles Scribner's Sons, 1898), p. 392.]

changes that result from injuries, functional changes, and the influence of the environment could be explained only by making a major assumption. One would need to assume that the parts of the soma affected altered the germ-plasm in the sex cells of the given individual in such a way that a descendant arising from one such sex cell manifested precisely those changes which had resulted from external influences in the corresponding parts of the parent organisms.

Weismann could conceive of only two ways in which the germ-plasm might be adequately altered. Either we assume that special paths lead from all parts of the body to the gonads, along which information about somatic changes can reach and appropriately change the gametes, or we assume, along with Darwin, that each cell liberates gemmules, which are transferred by the circulatory system and combine with the germ-plasm of the sex cells. "Thus either the presence of hypothetical tracks along which a modifying, though totally inconceivable, influence might be transferred to the germ-cells, or else the discharge of material particles from the modified organ, must take part in the formation of the germ-plasm: there is no third way out of the difficulty."[37]

Concerning the first proposal, according to which the transmission pathways are nerves, Weismann pointed out that no one yet had dared explain how changed body parts could materially alter the germ-plasm in the appropriate manner via nerve impulses going to the sex cells. For this, one would have to imagine that each cell of the entire body was connected by nerve pathways with every sex cell of the ovary or testis and directly transmitted information about what happened to it, including orders that the germ-plasm conduct itself this or that way with respect to the state of each of millions of somatic cells. "I believe that it would be impossible to avoid absurdities in explanations of this kind, and consider the whole idea inadmissible."[38]

Turning to the hypothesis of pangenesis and noting that scientific progress had rendered "circulation of gemmules" improbable, Weismann considered the hypothesis unlikely not so much because "we must imagine that the gemmules are *given off,* and then *circulate* through the body, but principally on account of the implied *addition of gemmules*—i.e., of *primary* constituents—to the germ-plasm of the germ-cells!" Weismann noted that the germ-plasm was not formless but organized into special structures in the nuclei of cells—"nuclear rods" or "idants"[39]—which maintained a constancy in number and form even while passing through the complex process of division, during which they underwent the longi-

[37] *Ibid.*, p. 515 [*Ibid.*, p. 393.]

[38] *Ibid.*, p. 517 [*Ibid.*, p. 394.]

[39] [*Ibid.*, p. 394.] The term "chromosome," which Wilhelm von Waldeyer introduced in 1888, was at that time still not in general use.

tudinal splitting that assured the uniform distribution of the material they contained. These nuclear structures argued against a continuous flow of hereditary material to the germ-plasm.

"It is impossible to assume the transmission of somatogenic variations in any theory which accepts the nuclear substance of the germ-cells as germ-plasm or 'hereditary substance'; for it is theoretically impossible to account for these variations, no matter how ingeniously the theory is constructed."[40] From the beginning of the 1890s on, Weismann clearly saw the incompatibility of the concept of determinants of hereditary traits localized in the structured components of cell nuclei with the assumption of the inheritance of acquired traits. This concept of structured heredity components was later called the chromosome theory of heredity. As Nikolai Ivanovich Vavilov wrote, "The chromosome theory was a very great contribution to biological science, leading scientists of heredity from speculative thinking to the sphere of precise experimental facts which could guide researchers to a materialistic understanding of a most difficult area in biology."[41]

Although at that time it was not proven by rigorous experiments, Weismann, in *The Germ-plasm,* came to a completely warranted conclusion. He claimed that "*all permanent—i.e., hereditary—variations of the body proceed from primary modifications of the primary constituents of the germ;* and that neither injuries, functional hypertrophy and atrophy, structural variations due to the effect of temperature or nutrition, nor any other influence of environment on the body, can be communicated to the germ-cells, and so become transmissible."[42]

Weismann repeated the same idea at the end of his book, after a detailed presentation of his quite speculative theory of the structure of the hereditary substance. "It is self-evident from the theory of heredity here propounded," he wrote, "that only those characters are transmissible which have been controlled—i.e., produced—by determinants of the germ, and that consequently only those variations are hereditary which result from the modification of several or many determinants in the germ-plasm, and not those which have arisen subsequently in consequence of some influence exerted upon the cells of the body. In other words, it follows from this theory that *somatogenic or acquired characters cannot be transmitted.*"[43] In order correctly to understand Weismann's views, it is extremely important to note the assertion directly following the above-

[40] *Ibid.*, p. 518 [*Ibid.*, 395.]

[41] Nikolai Ivanovich Vavilov, *Tomas Gent Morgan. Izbr. trudy v piati tomakh* [*Thomas Hunt Morgan: Selected Works in Five Volumes*] (Moscow: 1965), V, 730.

[42] Weismann (n. 23), p. 518. [Translation taken from (n. 36), p. 395.]

[43] *Ibid.*, p. 608. [*Ibid.*, p. 462.]

cited words: "This, however, does not imply that external influences are incapable of producing hereditary variations; on the contrary, they always give rise to such variations when they are capable of modifying the determinants of the germ-plasm."[44] And further on: "The primary cause of *variation* is always the effect of external influences.... When these deviations only affect the soma, they give rise to temporary nonhereditary variations; but when they occur in the germ-plasm, they are transmitted to the next generation and cause corresponding *hereditary variations in the body.*"[45]

It will be necessary to return later to these thoughts of Weismann while discussing the incorrect evaluations of his scientific legacy.

Weismann's efforts to free biology from the generally held hypothesis that the inheritance of acquired traits was possible and even necessary and his attempt to explain all evolutionary changes of form and function by natural selection led to a polemic principally involving Herbert Spencer—a philosopher widely but only superficially familiar with the biological literature.

Spencer's biological views bore the imprint of his general philosophical ideas, all of which had as their premise the idea of development. Defining phenomena of life as "uninterrupted adaptation of internal relationships to external relationships,"[46,47] Spencer conceived of the relationship between the changing environment and changing organisms as a process of compensation, which might be direct or indirect. He identified direct compensation, that is, the origin of changes under the direct influence of the external environment, with [the biological property of] adaptation. He proposed that a changed structure that had been caused by a change of function that in turn was a result of a change in the conditions of existence was transmitted by inheritance. Even at the outset of his book *Principles of Biology,* Spencer considered the position proven "that changes in structure produced by changes in function are transmitted to progeny,"[48] and in only one of the following chapters did he deem it necessary to give arguments for this assertion. Spencer clearly realized that it would not be easy to amass convincing evidence for the inheritance of acquired traits: "if the changes of structure worked in individuals by changes in their habits, are thus difficult to trace; still more difficult to trace must be the transmission of them... specialities of structure as are due to specialities of function,

[44] *Ibid.*, p. 608. [*Ibid.*, pp. 462–463.]

[45] *Ibid.*, p. 609 [*Ibid.*, p. 463.]

[46] Herbert Spencer, *Osnovaniia biologii* [*Principles of Biology*], trans. under editor A. Gerd (St. Petersburg, 1870), I, 57. [Translation taken from the Russian.]

[47] This idea is repeated in chapter 11 of Spencer's book.

[48] Spencer (see n. 46), p. 136. [Translation from the Russian.]

are usually entangled with specialities of structure that are, or may be, due to selection, natural or artificial.''[49] Spencer assigned to the category of inheritance of acquired traits changes in the structure of plants which occurred upon their transferal from certain climatic conditions to others, provided these changes were preserved in following generations.[50] He felt the same way about changes preserved in vegetative reproduction.

Spencer met with still greater difficulties in his search for proof of the inheritance of acquired traits in animals. He referred to examples used by Darwin, in which Darwin presumably explained the strengthened or weakened development of organs as due to use or disuse. The examples given included wings of domestic ducks, udders of milk cows and goats, pendent ears of domestic animals, and underdeveloped eyes in animals inhabiting the dark. Spencer cited communications from individuals about the inheritance of acquired traits without bothering to verify their credibility. Thus, among the proofs of ''acquired traits becoming directly hereditary'' were cited Louis's story about his puppy which learned to ''obey'' by itself, its mother having been taught this habit, and Doctor Brown's assertion that the children of people whose exterior changed in a hot climate tended to inherit similar changes.[51]

Spencer felt it necessary to posit a possible mechanism for transmission inheritance. For this goal he drew upon a concept he himself had introduced while describing the structure of an organism. This was the idea of hypothetical physiological units which lay intermediate between chemical units (molecules) and morphological units (cells).[52] The qualitative differences among these physiological units helped Spencer explain the hereditary differences among individuals of one species and the phenomena of hybridization, when ''traits of one parent are mixed with traits of the other.''[53]

While applying this hypothesis to an explanation of the inheritance of acquired traits, Spencer expressed himself cautiously. ''It is not equally manifest, *a priori*, however, that on this hypothesis, alterations of structure caused by alterations of function, must be transmitted to offspring. It is not obvious that change in the form of a part, caused by changed action, involves such change in the physiological units throughout the organism, that these, when groups of them are thrown off in the shape of reproductive

[49] *Ibid.*, p. 178. [Quotation found in *Principles of Biology*, 2 vols. (London: Williams and Norgate, 1884) I, 245.]

[50] Spencer did not specify under what conditions—new or original—the plants of the following generation develop.

[51] Spencer (see n. 46), p. 180. [Quotation taken from (n. 49), vol. 1, p. 248.]

[52] *Ibid.*, pp. 130-131. [*Ibid.*, pp. 182-183.]

[53] *Ibid.*, p. 185. [*Ibid.*, p. 254.]

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centres, will unfold into organisms that have this part similarly changed in form.''[54] Nevertheless, in speaking of ''changes of structure caused by changes of action,'' Spencer accepted the following ''general implication'': ''if an organism A, has, by any peculiar habit or condition of life, been modified into the form A′, it follows inevitably, that all the functions of A′, reproductive function included, must be in some degree different from the functions of A. . . . And if the organism A, when changed to A′, must be changed in all its functions; then the offspring of A′ cannot be the same as they would have been had it retained the form A.''[55]

Spencer's evolutionary views were closely bound to the *a priori* views proposed for direct adaptation, that is, to the acceptance of the inheritance of acquired characters. He allowed natural selection a leading role in evolution only at lower levels of the organic world. As the organization of living beings became more complex and their activity increased, however, he maintained that natural selection increasingly played a secondary role and that direct adaptation began to play a greater and greater role.

[54] *Ibid.* [*Ibid.*, p. 255.]

[55] *Ibid.*, p. 186. [*Ibid.*, pp. 255-256.]

This viewpoint brought Spencer into unreconcilable opposition to Weismann and Wallace, whose views specifically assigned the greatest role in evolution to natural selection.

The disagreement was reflected in a polemic started in 1886 by Spencer in the journal *Kosmos* in an article entitled "Factors of organic evolution," [56] and later continued in the *Contemporary Review,* a popular periodical. In these same years the English journal *Nature* carried polemical articles on the same theme, in particular articles contributed by the zoologist Edwin Ray Lancaster. "It has been held by several naturalists recently (whom I will call the anti-Lamarckians, and among whom I include myself) that it is necessary to eliminate from Mr. Darwin's teachings that small amount of doctrine which is based on the admission of the validity of Lamarck's second law. As everyone knows, Mr. Darwin's own theory of the natural selection of congenital variations in the struggle for existence is entirely distinct from Lamarck's theory, and the latter was only admitted by Darwin as being possibly or probably true in regard to some cases, and of minor importance. . . . Those who think Lamarck's second law to be true have been urged to state (1) cases in which the transmission of acquired characters is directly demonstrated, or (2) cases in which it seems impossible to explain a given structure except on the assumption of the truth of that law. If they fail to do this, they are asked to admit that Lamarck's second law is unproven and unnecessary." [57]

In early 1893, Spencer printed in the *Contemporary Review* a long article, "The Inadequacy of '*natural selection*'". [58] In the same journal George John Romanes reacted to Spencer's views on natural selection but limited his comments to particular questions. [59] In the May issue of the *Contemporary Review* Spencer published a second article on the same round of questions, [60] and in the July issue there appeared still another

[56] Herbert Spencer, "The Factors of Organic Evolution," Kosmos, 1886, p. 241.

[57] Edwin Ray Lankester, "The Inheritance of Acquired Characters," *Nature,* 1889-90, *41:* 414-416. [This note was a response to the preceding note by Herbert Spencer bearing the same title.]

[58] Herbert Spencer, "The Inadequacy of Natural Selection," *Contemp. Rev.,* Feb. and March, 1893, *63:* 152-166, 439-456.

In the same year a Russian translation of this article was published in the journal *Nauchnoe obozrenie* [*Science Review*]. The editor of this journal was Mikhail Mikhailovich Filippov, who actively propagandized in Russia the idea of the inheritance of acquired traits. A year later a second edition of the brochure was published. References to Spencer's article are given below according to the second edition.

[59] George John Romanes, "Mr. Herbert Spencer On Natural Selection," *Contemp. Rev.,* April, 1893, *63:* 499-517. As Weismann noted, Romanes "never finally broke with the idea of the inheritance of acquired traits and therefore could not make all the necessary deductions regarding Spencer's views." Weismann (n. 12), p. 55.

[60] Herbert Spencer, "Professor Weismann's Theories," *Contemp. Rev.,* May, 1893, *63:* 743-760.

article by Romanes specially devoted to the polemic between Spencer and Weismann.[61] In September of the same year Weismann's article, "The all-sufficiency of natural selection," was published in German as a separate work. It appeared in English in the *Contemporary Review* that same month and was followed by Spencer's "A Rejoinder to Professor Weismann." [62]

There is no need to present and discuss Spencer's objections to the theory of natural selection as the main explanatory principle of evolutionary change. Suffice it to say he thought that the phenomena of adaptive correlative changes, "coadaptation," presented a problem for Weismann's theory. As Spencer wrote, "If . . . modifications of structure produced by modifications of function . . . are in any measure transmissible to descendants, then all these coadaptations, from the simplest up to the most complex, are accounted for." [63] This article contains the aphorism which Spencer repeated so often thereafter: "Either there has been inheritance of acquired characters, or there has been no evolution." [64]

Not limiting himself to theoretical arguments, Spencer strove also to introduce factual proof of the inheritance of acquired traits. In particular, he devoted much space to the phenomenon soon to be called telegony. [65] This was a form of reversion often described in the literature of animal breeders. It entailed the belief that a previous mating could influence the traits of the progeny of a later mating with a different sire. The fact that children of a widow's second marriage do not resemble her first husband, which might be expected if telegony was valid, led Spencer at first to be skeptical of the whole phenomenon. In his polemic with Weismann, however, telegony seemed to be a decisive argument for Spencer, and apparently he was loathe to dispense with it.

Spencer's article was accompanied by a wordy "Postscript" in which he returned to the question of telegony. He made reference to "a distinguished correspondent" from the United States who related the following incident: "children of white women by a white father, had been *repeatedly* observed to show traces of black blood, in cases when the woman had previous connection with a negro." In another passage Spencer described hosting another "American" who said that "in the United States there was an established belief to this effect." "Not wishing, however, to depend on

[61] George John Romanes, "The Spencer-Weismann Controversy," *Contemp. Rev.,* July, 1893, *64:* 50-53.

[62] Herbert Spencer, "A Rejoinder to Professor Weismann," *Contemp. Rev.,* 1893, *64:* 893-912. For the Russian translation, see n. 71.

[63] Herbert Spencer, *Nedostatochnost' estestvennogo otbora* [*The Inadequacy of Natural Selection*] (St. Petersburg, 1894), p. 28. [English passage appears on pp. 27-28 (n. 58).]

[64] *Ibid.,* p. 29. [*Ibid.,* p. 30.]

[65] See chapter 4 of this work.

hearsay," Spencer continued, "I at once wrote to America . . . Professor Marsh . . . sends a preliminary letter in which he says:—'I do not myself know of such a case, but I have heard many statements that make their existence probable.' . . . Dr. W.J. Youmans of New York . . . interviewed several medical professors, who, though they have not themselves met with instances of such facts, say that the alleged result, described above, 'is generally accepted as a fact.'"[66]

The origin of such stories is completely understandable in light of the attitude of many American whites toward Negroes. Spencer must have had a very strong desire to establish the facts of telegony since he treated these unverified and tendentiously racist stories with such credulity. He also made references to the textbook of the American physiologist Austin Flint, who presented analogous, third-hand information.[67] Spencer concluded, "We must take it as a demonstrated fact that, during gestation, traits of constitution inherited from the father produce effects upon the constitution of the mother; and that these communicated effects are transmitted by her to subsequent offspring. We are supplied with an absolute disproof of Professor Weismann's doctrine that reproductive cells are independent of, and uninfluenced by, somatic cells; and there disappears absolutely the alleged obstacle to the transmission of acquired characters."[68]

In their search for arguments to buttress the possibility of hereditary changes in sex cells wrought by the influence of the altered soma, the supporters of the inheritance of acquired traits have referred to the imaginary phenomenon of telegony right up to recent times. They have cited the scientifically unverified opinions of laymen rather than precise experiments. Khila Faivilovich Kushner in particular followed this practice. "Zootechnical practice in the field of horse and dog breeding," he wrote, "has long attributed great significance to the matter of what sire is mated with a young mare or bitch, believing that an unfortunate choice of sire for the first pregnancy may harm the breeding value of the female parent."[69] These opinions of Kushner and similar ones of Nuzhdin, who also accepted the possibility of telegony (see chapter 4), do not correspond to contemporary standards of science. Several years later N.I. Feiginson also cited long-discredited communications regarding the supposed influence of previous matings on traits of progeny born later of another sire.[70]

[66] Spencer (n. 63), p. 57. [(n. 58), pp. 60-61.]

[67] Austin Flint, *A Textbook of Human Physiology* (4th ed; New York, 1888).

[68] Spencer (n. 63), p. 59. [Passage could not be found in English text.]

[69] Khila Faivilovich Kushner, "O iavleniiakh kseniinosti i telegonii u zhivotnykh" ["On Phenomena of Xenia and Telegony in Animals"], *Zhurn: obshchei biol.* [*Journal of General Biology*], 1949, *10:* 212.

[70] Concerning this, see: D.V. Lebedev, M.S. Navashin, Iu. M. Olenov, *Vestn. Leningr. un-ta* [*Leningrad University Herald*], 1956, *No. 21:* 135-143.

As stated above, in September 1893 Weismann published a small book, polemically entitled *The All-sufficiency of Natural Selection.*[71] This served as a reply to Spencer's article. First Weismann noted that although his views about the noninheritance of acquired traits were espoused by certain authors, his conclusions incited many objections and were not yet universally accepted. Some of Weismann's opponents took the *a priori* position that acceptance of the inheritance of acquired traits was an essential, integral part of evolutionary belief and therefore was necessary for the evolutionist. Others thought that inheritance of acquired traits could be proven by facts. In Weismann's opinion the source of confusion bred by such views lay above all in the lack of a precise definition for the very notion of "acquired trait." Some of Weismann's critics saw convincing arguments against his theoretical views in the experience of animal breeders. Answering one such critic, Martin Wilckens,[72] Weismann wrote that "somatogenic" or "acquired" changes were not just any changes but only those that resulted from changed functions, that is, those that resulted from the use or disuse of organs. Weismann believed that parts of the organism could be changed in a dual manner: (a) through changes in the hereditary constitution, in which case the change of traits perceivable by the observer appears only in following generations, and (b) by intensified or diminished use of the respective parts. Weismann disputed the inheritance of the second category of change. He thought that climatic influences, if they affected only the soma, also belonged to the second category.

A most convincing example which, according to Wilckens, argued against Weismann's views was the rise of the pure/bred English horse. "By means of continued exercise in the riding school and breeding of the fastest horses," wrote Wilckens, "the progeny are completely changed in body form. The head has become smaller, the ears longer, and the frame higher." Citing this quotation, Weismann remarked, "I see nothing in this example that speaks in support of the inheritance of 'somatogenic' traits. . . . It is simply *petitio principii*. . . . It was not horse racing over 200 years that transformed the ordinary horse into the race horse but the selection of the most advantageous variations for racing from among progeny of the best runners."[73] Weismann did not consider it necessary to refute all the

[71] Weismann (n. 12). M.M. Filippov printed a partial translation of this article in *Nauchnaia biblioteka* [*Science Library*], a supplement to the journal *Nauchnoe obozrenie* [*Science Review*], under the general title, "Veisman i Spencer. Estestvennyi podbor. A. Veisman, vsemogyshchestvo estestvennogo podbora. H. Spencer, Otvet Weismanu" (St. Petersburg: 1894) ["Weismann and Spencer: Natural Selection. A. Weismann, 'The All Sufficiency of Natural Selection. "H. Spencer 'Rejoinder to Weismann.'"] [For the full English titles see n. 12 and n. 62.]

[72] Martin Wilckens, "Die Vererbung erworbener Eigenschaften von Stankpunkte der landwirtschaftlichen Tierzucht in Bezug auf Weismann'schen Theorie der Vererbung," *Biol. Zbl.*, 1893, *13:* 420.

[73] Weismann (n. 12), p. 4. [Wilckens is quoted in the German edition but not in the English.]

supposed proofs of inheritance of acquired characters. "Were I to refute all that have hitherto been advanced," he wrote, "new ones would assuredly be constantly forthcoming, and so arguing in this way, we should hardly come to a conclusion."[74]

One of the objections Spencer made against Weismann concerned the correlative changes mentioned above. Spencer refused to attribute a spontaneous and mutually independent appearance of changes in various parts of the body to natural selection. It seemed completely clear to him, for example, that the increase in size of horns in deer was accompanied by a simultaneous thickening of the skull, strengthening of the socket ligaments and muscles of the neck and back, and that all these results of exercise would be inherited. "I should not be surprised," Weismann noted concerning Spencer's point, "if many who read his article.... should be carried away by the strength of his skillful representation, and hold the *easier* explanation of the facts —by the inheritance of acquired characters— to be the *correct* one."[75]

Concerning these arguments of Spencer, Weismann noted that the exercise of muscles indeed strengthens them and inactivity weakens them. It was a natural idea therefore to assume that the insufficient development of unused muscles, for example, is transmitted to following generations. This assumption was refuted, however, in the case of passively functioning parts, such as the carapace of insects and crustaceans which serve as mechanical protection and, in the case of certain insects, as protective coloration. In the process of evolution such parts which earlier were useful can become less developed if they become superfluous.

Weismann examined with particular care the adaptive traits of underdeveloped females among the social insects, e.g., worker bees and worker and soldier ants. Even if the adaptive traits that are useful for the species arose as the result of intensified use of this or that part, they cannot be passed on to their progeny, since the bearers of those traits do not themselves leave progeny. The males and females which are reproductively functional and which produce the progeny among social insects are devoid of the aforesaid traits. "None of these changes," wrote Weismann, "can rest on the transmission of functional variations, as the workers do not at all, or only exceptionally, reproduce; they can thus only have arisen by a selection of the parent ants dependent on the fact that those parents which produced the best workers had always the best prospect of the persistence of their colony. No other explanation is conceivable; and it is just because no other explanation is conceivable that it is necessary for us to accept the principle of natural selection. It alone can explain the adaptations of organisms without assuming the help of a principle of design."[76]

[74] *Ibid.*, p. 10. [*Ibid.*, p. 311.]

[75] *Ibid.*, p. 13. [*Ibid.*, pp. 312-313.]

Summarizing his understanding of the development of special adaptations among worker ants, Weismann asked on what basis can we regard selection as the factor which creates these adaptations. "The answer is very simple: with the same right as we have for believing in its activity anywhere else in nature.... For there are only two possible *a priori* explanations of adaptations for the naturalists—namely, the transmission of functional adaptations and natural selection; but as the first of these can be excluded, only the second remains."[77]

In other passages from the same essay Weismann claimed, "We may thus be able to prove by exclusion the reality of natural selection."[78] "Accordingly I hold it to be demonstrated that all hereditary adaptation rests on natural selection, and that natural selection is the one great principle that enables organisms to conform, to a certain high degree, to their varying conditions, by constructing new adaptations out of old ones."[79] "Progress in science usually involves a struggle against deep-rooted prejudices: such was the belief in the transmission of acquired characters; and it is only now that it has fortunately been overcome that the full significance of natural selection can be discerned. Now, for the first time, consummation of the principle is possible; and so my work has not been to exaggerate, but to complete."[80]

Regarding the examples of the origin and fixation of adaptive traits in social insects, and among worker ants and bees in particular, Weismann wrote, "It is difficult to imagine selection which works by such a roundabout path, but we should consider this explanation as correct, since it is the only one possible."[81]

On the basis of this he asserted that "harmonious and efficacious metamorphosis of many co-operative parts [as Spencer termed them] can proceed without any concurrence of the transmission of acquired characters.... I can only explain Mr. Spencer's ignoring of such cogent instances," Weismann commented without irony, "by supposing that as a

[76] *Ibid.*, p. 25. [*Ibid.*, pp. 318-319.] Seidlitz had already clearly shown the impossibility of using the inheritance of acquired traits to explain polymorphism in social insects.

[77] *Ibid.*, p. 58. [*Ibid.*, p. 336.]

[78] *Ibid.*, p. 61. [*Ibid.*, p. 337.]

[79] *Ibid.*, p. 62 [*Ibid.*, p. 338.]

[80] *Ibid.*, pp. 63-64. [*Ibid.*, p. 338.]

[81] Weismann was so fascinated by the idea of natural selection as the omnipotent motive force of evolution, that he hypothetically extended the activity of this force beyond its lawful application. In particular, he thought that the struggle for existence (and as its consequence, the survival of the best adapted) took place not only between individuals, but between the parts of each individual. Since discussion of all sides of Weismann's evolutionary views is not the task of this book, here it suffices to point out the incorrectness of his concept of struggle among parts of the organism. [Quotations are taken from the Russian.]

philosopher, he is unacquainted with the facts by personal observation."[82]

In contrast to Spencer, entomologists, especially those who studied bees, e.g., Grigorii A. Kozhevnikov[83] and Vladimir V. Alpatov, and who could cite their own research, fully supported Weismann's views on the origin of polymorphism in social insects. In particular, Alpatov wrote, "the reason it is impossible to evoke the principle of the inheritance of acquired traits to explain adaptive traits in bees is that worker bees take practically no part in the continuation of the species."[84]

Weismann also devoted several pages to the question of telegony, which Spencer regarded as "an absolute refutation of Weismann's teaching." Besides the theoretical considerations which indicate the impossibility of previous matings influencing the progeny of a later mating, Weismann referred to the work of H.G. Settegast, H. von Nathusius, and Kühn, who had demonstrated the absence of telegony. It is well known that James Cossar Ewart established the same absence with complete rigor in experiments conducted from 1896 to 1901.

It is interesting to consider how Weismann was presented to the Russian reading public. Mikhail M. Filippov took it upon himself to fulfill that task and did so more in accordance with his personal scientific tastes than with requisite objectivity. Not being a biologist he naturally could not base his opinion on personal research but only on his study of the pertinent literature. If one were to judge from his essays alone, one would have to say that Filippov possessed an unshakeable belief in the necessity of the inheritance of acquired traits. It is quite natural that Spencer's ideas, from which he probably took his own views, were agreeable to Filippov. He therefore published in full Spencer's polemical article directed against Weismann, as well as the lengthy postscript. He supplied neither one with editorial comments. Filippov dealt differently with Weismann's reply. Of the ninety-six pages of the German text, Filippov printed in Russian fewer than twenty-eight, noting in an editorial comment that in Weismann's brochure "there is so much discussion, much of it of a personal character, that we limited ourselves to a thorough excerpting, yet we convey all the essence of the matter."[85] Considering this remark, it is instructive to quote the following passage from Spencer's article. "Toward the close of my salmon-fishing days, I used to observe what a bungler I had become in putting on and taking off artificial flies,"[86] or "notwithstanding

[82] Weismann (n. 12), p. 17. [*Ibid.*, pp. 314, 317.]

[83] Grigorii Aleksandrovich Kozhevnikov, *Materialy po estestvennoi istorii pchely* [*Material on the Natural History of Bees*] (Moscow: 1905).

[84] Vladimir Vladimirovich Alpatov, *Porody medonosnoi pchely i ikh ispol'zovanie v cel'skom khoziaistve* [*Breeds of Honey Bees and Their Use in Agriculture*] (Moscow: 1948) p. 118.

[85] Weismann (n. 71), p. 3.

[86] Spencer (n. 63), p. 5 [Passage taken from the English, p. 3.]

experiences showing the futility of controversy for the establishment of truth, I am tempted here to answer opponents at some length. But even could the editor allow me the needful space, I should be compelled, both by lack of time and by ill health, to be brief."[87] Brief Spencer never could be, but Filippov begrudged no space in his publication in reproducing all of Spencer's discussion. Besides that, Filippov accompanied the publication of Weismann's article with his own numerous and rather lengthy comments. From them the reader might learn, for instance, that "Weismann cited no convincing facts in support . . . of the influence of climate," that "[Weismann's] final deduction was completely unfounded," that "frequent trimming of toenails and hair speeds their growth," that "the one who asserts the opposite is obliged to prove his position," and more in the same vein.

These comments (all made in the same peremptory tone) were summoned to convince the reader that the philosopher Spencer and the publisher Filippov could fathom special biological questions more deeply than could the qualified biologist Weismann, who incidentally had occupied a university chair for over a quarter century.

Filippov not only propagated Spencer's Lamarckian views by publishing his polemical articles, but he defended these views in his own essays and particularly in his book *Philosophy of Reality,* which was popular in its time. Filippov's temperamental judgments on questions of biology, especially while defending the inheritance of acquired traits, testified to his multifaceted education, but they also conveyed an indelible tarnish of dilettantism. On this note, thereofore, we will stop.

Pëtr Frantsevich Lesgaft, building his whole course on the functional principle, defended Lamarckian ideas on a higher plain in his lectures on anatomy. Still more significant in familiarizing the Russian reading public with Lamarckian ideas was a long article, "Lamarck and his teaching,"[88] published in 1896 by Lesgaft's co-worker, the botanist-physiologist and pedagogue-methodist, Valerian Viktorovich Polovtsev. Here Lamarck's evolutionary views were presented conscientiously and in detail but without critical discussion. The article had still greater significance from the fact that at that time none of Lamarck's essays had yet been published in Russian translation. With reference to Lamarck's position favoring the inheritance of acquired traits, found in his *Zoological Philosophy,* Polovtsev gave no supporting evidence but simply quoted Lamarck's words that this position "contains the indisputable truth."[89]

[87] *Ibid.*, p. 59. [*Ibid.*, p. 63.]

[88] Valerian Viktorovich Polovtsov, "Lamark i ego uchenie" ["Lamarck and His Teaching"], *Izv. SPb., biol. labor.* [*St. Petersburg News, biological laboratory,*] 1896, *1:* no. 3, pp. 16–46, no. 4, 7–50.

[89] The article, cited above, by Polovtsov and his relation to the teaching of Lamarck are thoroughly examined in the book by Boris Eugenievich Raikov, *Valerian Viktorovich Polov-*

(*contd.*)

In the 1890s Russian readers could form some impression of the connection between the problem of evolution and the question of the inheritance of inborn and acquired traits through a translation of Romanes's popular-science book. Romanes discussed the views of Erasmus Darwin, Lamarck, and Spencer concerning "the cumulative transmission of functionally-produced or otherwise 'acquired' modifications." He pointed out that one cannot come close to applying the principle of use and disuse to all organs and parts of the body, that "recently, the significance of Lamarck's theory is blemished by that circumstance, and serious doubts have arisen as to whether acquired traits can be inherited." [90]

After this digression, we must return to the polemic between Weismann and Spencer, which Weismann, drawing upon new factual data, took up again in his treatise on *The Effect of External Influences upon Development.* At the same time Weismann replied to Oscar Hertwig's polemical essay [91] that appeared while his treatise was in press. In the foreword Weismann wrote, "My opponent . . . may rest assured that regarding the influences of external conditions, I am not completely blind." [92] With excess straightforwardness Weismann insisted that external influences are not the active cause (*causa efficiens,* in the Aristotelian sense) of the origin of various forms but only the factor responsible for the realization of the potentialities of development inherent in the organism. Exaggerating the performationist side of development in deference to the epigenetic side, an emphasis which Hertwig justifiably objected to, Weismann once again promoted the role of natural selection in evolution.

Weismann returned to problems of heredity and specifically to the question of the inheritance of acquired traits, in his widely known *Lectures on Evolutionary Theory* (1903; the third and last edition published during his lifetime came out in 1915). Here he once more insistently asked the question which exposed the insuperable difficulty for any Lamarckian theory: "How then could the changes which take place in a muscle through exercise, or in the degeneration of a joint in consequence of disuse, communicate themselves to a germ-cell lying inside the body, and do so in such a fashion that this germ-cell is able, when it grows into a new organism, to produce of itself, in the relevant muscle and joint, a change the same as that which had arisen in the parent through use and disuse? That is the

tsov. Ego zhizn' i trudy [*Valerian Viktorovich Polovtsov: His Life and Work*] (Moscow-Leningrad: 1956). chapter 4.

[90] George John Romanes, *Teoriia Darvina i vazhneishie iz ee primenenii* [*Darwin's Theory and Its Most Important Applications*], trans. N.K. Kol'tsov, ed. M.A. Menzbir (Moscow, 1889), pp. 198-199. [This reference is to Romanes's *Darwin, and After Darwin,* 2 vols. (Chicago: Open Court, 1895) I, 255-256; the second part of the quotation could not be identified.]

[91] Oscar Hertwig, *Zeit- und Streitfragen der Biologie. Pt. I. Präformation oder Epigenese? Grundzüge einer Entwicklungstheorie der Organismen,* (Jena: Gustav Fischer, 1894).

[92] August Weismann, *Äussere Einflusse als Entwicklungsreize* (Jena: Gustav Fischer, 1894).

question which forced itself upon me very early, and in following it up I have been led to an absolute denial of the transmission of this kind of 'acquired characters.'" [93]

In answer to his opponents' objections to his view of the localization in the cell nucleus of the material factors of heredity, Weismann wrote, "thus the argument used by those who deny the existence of a hereditary substance would be paralleled if we denied that Man possesses a thinking substance, and maintained that he thinks with his whole body, and even that the brain cannot think by itself without the body." [94]

Weismann was also reproached for allegedly maintaining the absolute immutability of the germ-plasm: "I have been frequently and persistently credited with maintaining that the germ-plasm is invariable—a misunderstanding of my position, due perhaps to a somewhat too brief and terse statement which I made at an earlier period (1886). I had described the germ-plasm as 'a substance of great power of persistence,' and as varying with difficulty and slowly, basing this statement upon the age-long persistence of many species in which the specific constitution of the germ-plasm must have remained unchanged. . . . But at no time was I unaware that the whole phyletic evolution of the organic world is only conceivable on the assumption of continual variation of the germ-plasm, that it actually depends upon this." [95]

Next there follows a most interesting thought. Weismann insisted that it was essential to "understand how the germ-plasm may be variable, and yet at the same time remain unvaried for thousands of years, how it is ready and able to furnish any variation that is possible in species if that is required by external circumstances, and yet is able to preserve the characters of the species in almost absolute constancy through whole geological ages; in short, how it can be at once readily variable and yet slow to vary." [96,97]

[93] Weismann (n. 31), vol. 1, pp. 206-207. [Quotations taken from the English: *The Evolution Theory,* trans., J. Arthur Thomson and Margaret R. Thomson, 2 vols. (London: Edward Arnold, 1904), vol. 1, p. 251.]

[94] *Ibid.,* vol. 1, p. 280. [*Ibid.,* vol. 1, p. 340.]

[95] *Ibid.,* vol. 2, pp. 175-176. [*Ibid.,* vol. 2. p. 195.]

[96] *Ibid.,* vol. 2, p. 176. [*Ibid.,* vol. 2, p. 196.] Almost seventy years later, armed with the evolutionary theory of the second half of the twentieth century, molecular genetics, and cybernetics, only Schmalhausen expressed the same thought, "The structure of the hereditary 'code' is actually rather well protected. Only harsh changes in external factors, especially very unusual (chemical, radiation) influences, cause destruction of the hereditary structure, resulting in new mutations." Ivan Ivanovich Schmalhausen, "Reguliruiuschchie mekhanizmy evoliutsii. K 100-letiiu teorii estestvennogo otbora" ["Regulatory Mechanisms of Evolution: On the Centennial of the Theory of Natural Selection"], *Zool. Zhurn.* [*Zoological Journal*], 1958, 37. no. 9, 1958.

[97] Reprinted in the book by Ivan Ivanovich Schmalhausen, *Kiberneticheskie voprosy biologii* [*Cybernetic Questions of Biology*] (Novosibirsk: 1968), p. 26.

Weismann's conceptions of the motive force of evolution, of the factors of heredity, and of the manner of action of natural selection, were objectively and comprehensively presented in two books devoted to phenomena of heredity and the history of evolutionary teachings by Yurii A. Filipchenko. In the latter of these books Filipchenko wrote about the historical

Yurii Aleksandrovich Philiptschenko (Filipchenko)
(1882-1930)

significance of Weismann's work, "Relatively recently it was still acceptable to criticize strongly Weismann's theory, pointing out its weaknesses . . . For all that, however, its significance is very great, and one cannot deny that its influence on the elaboration of our modern views has been very significant. Weismann's principle service was his refutation of that naive Lamarckism which had been a widespread belief, that is, the belief in the inheritance of acquired traits in the sense of somatic induction (inheritance of injuries, results of exercise and non-exercise of organs, etc.)."[98] Filipchenko emphasized the importance of Weismann's concept that change in

[98] Yurii Aleksandrovich Filipchenko, *Nasledstvennost'* [*Heredity*] (Moscow: 1917; 2nd ed., Petrograd: 1923). Filipchenko, *Evoliutsionnaia ideia v biologii. Istoricheskii obzor evoliutsionnykh uchenii XIX veka* [*Evolutionary Ideas in Biology: An Historical Outline of Evolutionary Teachings of the 19th Century*] (Moscow: 1923), pp. 222–223.

the heredity material of sex cells was the source of evolutionary changes and of his doctrine of determinants, from which developed the concept of factorial inheritance, the gene concept of modern genetics. In a summary Filipchenko claimed, "Weismann must be recognized as one of the greatest figures among all the proponents of evolutionary theory of the second half of the nineteenth century."

Weismann's views, which generated such a widespread polemical literature, were not only disputed but often distorted. It was earlier pointed out that Weismann considered his doctrine of the germ-plasm, transmitted without interruption from generation to generation across successive generations of sex cells, as the antithesis of the inheritance of acquired traits. Weismann sometimes referred to this continuity as the potential immortality of the germ-plasm since it was not created anew in each generation by the somatic part of the individual, which in contrast had a limited lifetime. By this, of course, he meant nothing more than that the germ-plasm could exist as long as the line of generations existed.[99,100]

It is well known that William Bateson, Jan Paulus Lotsy, and other autogenecists unjustifiably attributed to Weismann a belief in the absolute immutability of the germ-plasm and in the independence of the evolutionary process from the external environment. The theories of the autogenecists themselves could and did lead to very idealistic conclusions. It goes without saying that Weismann should not bear the responsibility for the factual and methodological mistakes of these authors.

In the Democratic Republic of Germany, co-workers of the Institute of Philosophy at the University of Berlin recently attempted properly to evaluate the scientific legacy of Weismann. In 1963, R. Löther gave a short resumé of his numerous theoretical works in the field. He pointed out that Weismann's creation of a theory of heredity was, "a means of establishing Darwinian theory as a synthesis of the processes of heredity, hereditary change, and selection. He . . . was the first to defend with total consistency the idea that heredity is based on the transmission of specific material factors carrying the hereditary potential from one generation to another (chromosome theory)."[101] Löther noted that Weismann's prediction in

[99] Oscar Hertwig understood Weismann's expression "immortality of the germ-plasm" in the same sense, and he several times wrote in opposition to Weismann's theory of heredity (the concept of determinants) and against his theory of development based on unequal hereditary division of the egg and the following generations of cells of the developing embryo. Despite his disagreement with many of Weismann's theoretical constructs, Hertwig did not object to Weismann's idea of the nonheritability of acquired traits. [In later works Hertwig came down on the side of the inheritance of acquired characters; see his *Allgemeine Biologie* (Jena: 1909), pp. 652–653.]

[100] Hertwig (n. 91), p. 72.

[101] Rolf Löther, "August Weismann—Wegbereiter des Darwinismus und wissenschaftlicher Vererbungslehre," *Wiss. und Fortschr.*, 1963, *10*: 463.

1887 of the necessity of a reductional division during gametogenesis,[102] later verified by cytologists, was indicative of the characteristic insight of his views on heredity. Löther wrote, "Weismann's objections to the Lamarckian hypothesis of functional inheritance (inheritance after use or disuse of organs) helped overcome in a fundamental way any false conceptions of phenomena of heredity."[103]

In an article devoted to contemporary evolutionary theory and a scientific picture of the world Löther wrote that "Weismann's ideas about heredity and evolution had a profound influence on the formation of biological theory. His views of natural history contain distinct elements of dialectical thinking. . . . The widely held . . . estimate of Weismann as the embodiment of reactionism, idealism, and metaphysics is contradicted by the facts."[104]

Similar ideas were developed in an article by K. Gebhardt devoted to the philosophical content of Weismann's biological theories. She also set herself the task of correctly evaluating his views. Gebhardt correctly thought that an examination of the whole complex of Weismann's work was needed to understand truly his historic role. As she pointed out, Weismann's opinions concerning the relationship between structure and function, the stability and mutability of the germ-plasm, the relation between the external and the internal, and the roles of necessity and chance, all have a dialectical character. Gebhardt refuted the unfounded accusations that Weismann was an idealist by showing that he resorted to materialistic principles in explaining ontogeny as well as phylogeny. He extended these principles to those areas of biology where, due to ignorance of the essential processes of life, one still found mystical interpretations, that is, in descriptions of life forces, direct influences, and the inheritance of acquired traits.[105] Gebhardt traced the evolution of Weismann's theoretical views from agnostic opinions in early works, that is, "On the mechanical concept of nature,"[106] to materialistic and dialectic ideas in his later essays, *Lectures on Evolutionary Theory,* in which he decisively refuted vitalistic and Lamarckian views.

Weismann found a true and highly authoritative ally in the person of Alfred Russel Wallace. As early as his communication read at the Linneaen Society on 1 June 1858, Wallace had espoused the idea of evolution of

[102] August Weismann, *Über die Zahl der Richtungskorper und ihre Bedeutung für die Vererbung* (Jena: Gustav Fischer, 1887).

[103] Löther (n. 101), p. 464.

[104] Rolf Löther, "Moderne Evolutionstheorie und wissenschaftliches Weltbild," *Einheit. Z. Theorie und Praxis wiss. Sozialismus,* 1965, pt. 2: 31–32n.

[105] K. Gebhardt, "Zum philosophischen Gehalt des biotheoretischen Werkes August Weismanns," *Dtsch. Z. Philosophie,* 1965, *13:* 1280–1292.

[106] August Weismann, *Studien zur Deszendenztheorie. II. Über die letzten Ursachen der Transmutation* (*IV. Über die mechanische Auffassung der Natur*) (Leipzig: Wilhelm Engelmann, 1878).

Alfred Russel Wallace
(1829-1913)

species by the struggle for existence and natural selection and had contrasted it with the evolutionary views of Lamarck. Wallace wrote, "the view here developed renders such an hypothesis quite unnecessary, by showing that similar results must be produced by the action of principles constantly at work in nature. The powerful retractile talons of the falcon- and the cat-tribes have not been produced or increased by the volition of those animals; but among the different varieties which occurred in the earlier and less highly organized forms of these groups, *those always survived longest which had the greatest facilities for seizing their prey.* Neither did the giraffe acquire its long neck by desiring to reach the foliage of the more lofty shrubs, and constantly stretching its neck for the purpose, but because any varieties which occurred among its antitypes with a longer neck than usual *at once secured a fresh range of pasture over the same ground as their shorter-necked companions, and on the first scarcity of food were thereby enabled to outlive them.*"[107]

[107] Alfred Wallace, "O stremlenii raznovidnostei k neogranichennomu otkloneniu ot pervonachal'nogo tipa" ["On the Tendency of Varieties to Depart Indefinitely from the Initial Type"], in Charles Darwin, *Soch.* [*Works*], 1939, 3: 251. [The English text is reprinted in Charles Darwin and Alfred Russel Wallace, *Evolution by Natural Selection,* ed. Gavin de Beer (Cambridge: Cambridge University Press, 1958), pp. 277-278].

Both Wallace and Darwin were puzzled by the question of the cause of changes which after their appearance become the object of natural selection. When in 1868 Darwin tried hypothetically to solve that difficult question with the aid of his hypothesis of pangenesis, Wallace at first thought a solution had been found. He wrote that it was "a positive *comfort* to me to have any feasible explanation of a difficulty that has always been haunting me."[108] The relief, however, proved false. It is well known how skeptically Darwin later regarded his own hypothesis. Wallace also became disenchanted with it. Upon familiarizing himself with Weismann's work "The significance of sexual reproduction in the theory of natural selection," Wallace saw that it might prove necessary to reject both Lamarckism and pangenesis. After this, having become an adherent of Weismann, Wallace wrote, "The most remarkable steps yet made, in advance are, I think, the theory of Weismann of the continuity of the germ plasm, and its corollary that acquired modifications are never inherited."[109]

In 1889 Wallace's book *Darwinism* appeared and was soon translated into other European languages. A Russian translation by Mikhail Aleksandrovich Menzbir appeared in 1898 (the 2nd edition, to which references below are made, came out in 1911). In one of the last chapters of this book Wallace discussed the tendency that arose at the close of the nineteenth century to minimize the significance of natural selection. Theorists preferred to attribute the evolutionary process to changes in the form and structure of living beings under the influence of changing organ function (Spencer, Cope) or under the direct influence of the environment (Spencer, Semper) and the inheritance of those changes.

In essence, Spencer just exaggerated some concepts which Darwin himself accepted. Wallace cited the following excerpt from the concluding chapter of the *Origin of Species:* "[Modification of species] has been effected chiefly through the natural selection of numerous successive, slight, favourable variations; aided in an important manner by the inherited effects of the use and disuse of parts; and in an unimportant manner—that is, in relation to adaptive structures whether past or present, by the direct action of external conditions, and by variations which seem to us, in our ignorance to arise spontaneously."[110]

[108] James Marchant, ed., *Alfred Russel Wallace: Letters and Reminiscences*, vol. I (1916), p. 196, Quoted in Wilma George, *Biologist Philosopher. A Study of the Life and Writings of Alfred Russel Wallace* (London-Toronto-New York: Abelard-Schuman, 1964), p. 76.

[109] *Ibid.*, vol. 2, p. 41 Quotation from George, p. 257.

[110] Charles Darwin, *Proiskhozhdenie vidov* [*The Origin of Species*], *Soch.* [*Works*], 1939, *3:* 659. It should be mentioned that Menzbir's translation of this quotation is inaccurate. His version reads, "Inheritance of the results of exercise and non-exercise of organs had an insignificant effect. The direct action of the environment was also insignificant on those organs which show evidence of adaptation." Alfred Russel Wallace, *Darvinizm* [*Darwinism*] (2nd ed.; Moscow: 1911), p. 468.

Wallace disagreed with this view held by both Darwin and Spencer. In his opinion, "there is now much reason to believe that the supposed inheritance of acquired modifications—that is, of the effects of use and disuse, or of the direct influence of the environment—is not a fact"[111] Wallace considered it an important task to clarify whether the facts cited by Darwin, Spencer, and others did indeed require the recognition of the inheritance of acquired traits as a part of their explanation. Regarding changes in domestic animals, Wallace noted that their features, "have been subject to long-continued artificial selection, and we are so ignorant of the possible correlations of different parts, that the phenomena presented by them seem sufficiently explained without recurrence to the assumption that any changes in the individual, due to disuse, are inherited by the offspring."[112] Wallace explained the underdevelopment of wings in insular birds by the same process that Darwin suggested for the disappearance of wings in insular insects, namely "the destruction of those which, during the occasional use of their wings, were carried out to sea."[113] In a similar manner, he explained the loss of eyes in cave animals. "Whenever, owing to the total darkness, they became useless, they might also become injurious, on account of their delicacy of organisation and liability to accidents and disease; in which case natural selection would begin to act to reduce, and finally abort them."[114] Understanding the mechanism of the underdevelopment of hind limbs in whales and of wings in moas and cassowaries was problematical in Wallace's opinion since neither the intermediate forms nor the precise course of reduction of the organs was known. Wallace did not consider it necessary to regard disuse as the cause of the reduction of organs in these animals either. In a comment on this point, Wallace stated that he began to believe in the noninheritance of acquired changes upon his acquaintance with Weismann's views presented in "Nature" and later with his *Essays on Heredity,* translated by Edward Bagnall Poulton. Wallace also recalled that Francis Galton had spoken on the noninheritance of acquired characters quite a long time ago. In his article "A Theory of Heredity," Galton indicated the implausibility of the arguments in support of the inheritance of acquired characters. He referred to the same considerations which Weismann later presented.[115] Wallace then drew attention to the fact that the forms of atrophy of various organs in different animals are so dissimilar that they must not be explained by so simple and uniform a cause as the accumulation by inheritance of the results of the disuse of organs.

[111] Wallace (n. 110), p. 469.

[112] *Ibid.*, p. 471.

[113] *Ibid.*, p. 472.

[114] *Ibid.*, pp. 472–473.

[115] Galton, "A Theory of Heredity" (chapter 4, n. 57).

Wallace thought it yet more improbable that an intensified use of organs led to a fixed intensified development in descendants. For animals in the wild, the concept of the use of an organ was closely tied to the concept of its utility, and "utility is the constant subject for the action of natural selection."[116] In English this sounds more expressive because the words "use" and "utility" possess a common root.

The same reasoning could justly be applied to domestic animals except that utility for the animal was here replaced by utility for man and "natural" selection by "artificial." "Thus," wrote Wallace, "'the great and inherited development of the udders in cows and goats,' quoted by Spencer from Darwin, really affords no proof of inheritance of the increase due to use, because, from the earliest period of the domestication of these animals, abundant milk-production has been highly esteemed, and has thus been the subject of selection."[117]

Concerning the question of the results of the direct influence of the external environment, Wallace first of all noted that even though we do not doubt the influence of the environment in the production of changes, the assumption of the inheritance of such changes was "exceedingly doubtful, and Darwin nowhere expresses himself as satisfied with the evidence."[118]

Wallace very skillfully countered the attempts of American paleontologists, in particular Edward Drinker Cope, to replace the laws of evolution established by Darwin with "theoretical conceptions which have not yet been tested by experiments or facts, as well as metaphysical conceptions which are incapable of proof."[119] Wallace had in mind Cope's advocacy of the inheritance of the results of the use of organs and of his mysterious "bathmism" (for more detail, see chapter 6). He referred to the example Cope offered to demonstrate the change of organs through use, namely, the development in falcons and shrikes of hooked beaks armed with sharp tips. Wallace noted that Cope made no attempt "to show any direct causal connection between the use of a bill to cut or tear flesh and the development of a tooth on the mandible.... On the other hand, it is clear that any variations of the bill tending towards a hook or tooth would give the possessor some advantage in seizing and tearing its prey, and would thus be preserved and increased by natural selection."[120]

In dealing with Cope's assertion that the difference in digit number on the limbs of ungulates was due to the influence of different soils, Wallace

[116] Wallace (n. 110), p. 474. [Quotations are taken from Alfred Russel Wallace, *Darwinism. An Exposition of the Theory of Natural Selection with Some of Its Applications* (London: Macmillan & Co., 1889), p.417.]

[117] *Ibid.*, p. 474. [*Ibid.*, p. 417.]

[118] *Ibid.*, p. 476. [*Ibid.*, p. 419.]

[119] *Ibid.*, pp. 479–480. [*Ibid.*, p. 422.]

[120] *Ibid.*, p. 480. [*Ibid.*, p. 422.]

drew attention to the fact that the hereditary transmission of individual variations required in this explanation still awaited proof. "In the meantime it is clear that the very same results could have been brought about by variation and natural selection."[121] "Variation—in abundant or typical species—is always present in ample amount,... exists in all parts and organs... favourable variations are so frequently present that the unerring power of natural selection never wants materials to work upon."[122]

Karl Semper had amassed in his book vast amounts of material on the influence of various environmental factors—such as food, light, temperature, and the movement of air and water—on the morphological traits of animals.[123] Wallace pointed out that Semper, by his own admission, had failed to confirm empirically the idea of the accumulation through heredity of such changes. Wallace said that "there is hardly a single case adduced in the book which is not equally well explained by adaptation, brought about by the survival of beneficial variations."[124]

[121] *Ibid.*, p. 482. [*Ibid.*, p. 424.]

[122] *Ibid.*, p. 483. [*Ibid.*, p. 424.]

[123] Karl Gottfried Semper, *Die natürlichen Existenzbedingungen der Thiere*, 2 vols. (Leipzig: A. Brockhause 1880).

[124] Wallace (n. 110), p. 484. [(n. 116), p. 427.]

CHAPTER 8

Reviews Concerned with the Problem of the Inheritance of Acquired Characters (1920-1930)

The question of the inheritance of acquired characters was directly tied to the choice of a causal explanation of the evolutionary process: evolution on the basis of the Lamarckian principle of direct adaptation or on the basis of the Darwinian principle of natural selection. The significance of this choice was clearly explained at the beginning of this century by Kliment Arkad'evich Timiriazev. He wrote that "Neo-Lamarckians, e.g., like Wettstein, who assert that proving the existence of variability is also enough to explain the fact of adaptation, forget that the one does not in the least derive logically from the other." [1] Timiriazev noted that Haeckel as well as Wettstein was guilty of this unjustifiable linkage of variability and adaptation. "Other neo-Lamarckians, such as Henslow and Warming," Timiriazev continued, "arguing from the fact that many of the effects of external conditions turn out to be useful, conclude that there is no need to resort to selection, since conditions themselves act efficiently. This is the so-called doctrine of direct adaptation.... It is obvious that useful variations, which provide material for selection, must be included among those evoked by external conditions. It couldn't be otherwise. But to conclude conversely that external conditions in and of themselves must cause useful variations, is to create... an obscure and unfounded metaphysical theory of the environment.... Only one position is logically acceptable, that the physical action of the environment is independent of its results, that is, the result may be one of three types: beneficial, harmful, or indifferent.... If... in the grand total the majority of cases of modern organisms present us with examples of successful adaptations, then this is the result of an historical process which erased traces of failures and preserved only traces of successes, this is, the result of selection." [2]

It goes without saying that one could not decide the question with only

[1] Kliment Arkadievich Timiriazev, "Osnovnye cherty istorii razvitiia biologii v XIX stoletii" ["Basic Lines of the History of the Development of Biology in the 19th Century"] (1907), *Soch.* [*Works*], 1939, *8:* 121.

[2] *Ibid.*, pp. 121-122.

logical arguments, even given such convincing ones as Timiriazev's. What was required was to determine experimentally whether or not the Lamarckian concept of direct adaptation was valid. Adherents of this concept went to great lengths to try to prove experimentally the inheritance of acquired characters. The first of such attempts derive from the middle of the nineteenth century.

Summaries of the accumulated factual data appeared at the end of the nineteenth century and during the first three decades of the twentieth century.[3] During the 1920s and 1930s the number of these summaries increased significantly. Some of the reviewers presented the content of the experiments without critical comment; others simply assumed that the factual data was conclusive and went on to touch on the theoretical side of the issue.

In 1924 E.S. Smirnov, Iu. M. Vermel', and B.S. Kuzin published a book which represented the mechanistic-Lamarckian conception of evolution. The authors examined several cases, primarily drawn from the work of Paul Kammerer, who unreservedly regarded his experimental results as proof of the inheritance of acquired traits. Smirnov and co-authors evaluated Kammerer's experiments and other analogous experiments with the same prejudices. They did not cite the data of follow-up experiments which contradicted the originals. They did not even ask by what cytological or physiological mechanism the sex cells might be adaptively restructured under the influence of somatic changes, were such an influence proven to exist. The authors of this book even found it possible to agree with the assertion of Richard Semon, that the thickening of the epidermis on the soles of the human fetus developed "under the direct action of pressure," and that this observation provided "proof of the inheritability of functional changes." [4] They concluded, without any argumentation, that for Semon's observation "it is impossible to accept natural selection as the explanatory principle." [5] It is relevant here to recall that in discussing the same example Darwin displayed significantly greater caution in his judgment (see chapter 4).

In his review article "The Inheritance of Acquired Traits," J.A.

[3] For example, G.H. Theodor Eimer, *Die Entstehung der Arten auf Grund von Vererben erworbener Eigenschaften nach den Gesetzen organischen Wachsens* (Jena: 1888), 461 P.; George Henslow, *The Heredity of Acquired Characters in Plants* (London: 1908); Hans Przibram, *Experimental-Zoologie. 3. Phylogenie*, chapter 6, "Erwerbung von Eigenschaften und deren Vererbung" (Leipzig u. Wien: 1911), pp. 149-211; Richard Semon, *Das Problem der Vererbung "erworbener Eigenschaften"* (Leipzig: 1912); Paul Kammerer, *Neuvererbung oder Vererbung erworbener Eigenschaften. Erbliche Belastung und erbliche Entlastung* (Stuttgart u. Heilbronn; 1925).

[4] E.S. Smirnov, Iu. M. Vermel', and B.S. Kuzin, *Ocherki po teorii evoliutsii* [*Essays On the Theory of Evolution*], foreword by B.M. Zavadovskii (Moscow: 1924), p. 107.

[5] *Ibid.*, p. 109.

Detlefsen discussed in detail the phenomenon of the thickening of the skin on the soles of humans as well as the more demonstrative example of the formation of callouses on the carpus of the African warthog (*Phacochoerus*) and a number of similar phenomena. He said that the origin of these traits is *a priori* amenable to explanation from the Lamarckian as well as the Darwinian point of view. Detlefsen wrote, "Lamarckians say: 'See how a habit leads to the generation of appropriate inheritable determinants for the development of racial traits needed by the organism,' and the Weismannians reply: 'Pay attention to the way change in the germ-plasm leads to the origin of a structure which makes possible the development of the corresponding habit.'"[6] Detlefsen made the object of his review not the confirmation or refutation of the inheritance of somatic modification but an impartial evaluation of contrasting opinions. The Lamarckian scheme required that the sex cells undergo specific changes that would give rise to hereditary traits in the offspring that in turn would be identical to the somatic modifications in the parents. Detlefsen was forced to conclude that such specific germinal changes had not been confirmed beyond reasonable doubt. Moreover, as he concluded, "if somatic induction, and likewise parallel induction, were the usual *modus operandi* of evolution, we should expect to find many positive experimental proofs and not a handful of dubious instances."[7]

In 1926 Valerii Ivanovich Taliev discussed the issue of the inheritance of acquired characters in the chapter "Facts which seem to speak in support of Lamarckism," in his fine popular-science book. "Acceptance of Lamarck's basic views," wrote Taliev, "is possible only if it is established that changes caused in an organism by exercise or non-exercise or by the direct action of external conditions are inherited. But right here begins the unique tragedy of the Lamarckian position. That assumption, which neither Darwin nor Lamarck questioned has become in the present time a critical point of contention."[8] Taliev incisively proposed that "In order to allow theoretically the possibility of the hereditary transmission of changes which arise in organisms under the influence of external conditions, it is necessary to give a sufficiently lucid answer to the question: in what manner are these changes first transferred from the modified organ or tissue to the deeply hidden sex cells, imprinted on those cells, and then, during development of the new organism, reproduced in the same form in exactly the same location?"[9] Taliev examined an instance which had been

[6] J.A. Detlefsen, "The Inheritance of Acquired Characters," *Physiol. Rev.*, 1925, *5:* 249.
[7] *Ibid.*, pp. 274-275.
[8] Valerii Ivanovich Taliev, *Organizm, sreda i prisposoblenie* [*Organism, Environment, and Adaptation*] (Moscow, Leningrad: 1926), p. 143.
[9] *Ibid.*, p. 144.

Valerii Ivanovich Taliev
(1872-1932)

interpreted as the inheritance of an acquired behavioral trait: "Imagine how some complex action involving the nervous system and developing not only in space but in time can be transmitted to the hereditary substance, fixed in it, and then precisely reproduced in the following generation like a film strip. No scientific imagination can conjure this forth."[10]

Taliev turned to botanical examples which had been used as indirect arguments in support of the inheritance of acquired characters. One example he chose was the differential structure of leaves above and under water on the same half-submerged plant. He recalled that Lamarck, using the example of the water buttercup, had been the first to attempt to explain this phenomenon as the direct influence of the environment. Referring to Karl Goebel, Taliev wrote that, "the form of the underwater leaves of these flowering plants is none other than an early stage in the development of the same plant under normal conditions. In other words, underwater habitation does not transform the structure of the given species, but simply retards its development, retaining it in an immature state. Consequently, it was not water habitation that created the dissected underwater leaves, but on the contrary, the latter must have already existed in those plants which for some reason returned to a water environment."[11]

[10] *Ibid.*, p. 155.
[11] *Ibid.*, p. 154.

Edwin Grant Conklin
(1863-1952)

Taliev considered still another argument which was often mentioned in support of the inheritance of acquired characters. "However probable it may seem upon first glance that many benthic organisms lost their sight due to disuse, the question arises as to why exactly the opposite process takes place in a number of other such organisms, that is, a colossal increase in eye size? . . . Obviously, the path of evolution was guided not by the direct action of the environment but by some factor not directly subject to the environment, by properties of the organism itself."[12]

An interesting book by the American embryologist Edwin Grant Conklin first came out in 1914, and a Russian translation of one of the later editions appeared in 1928. Conklin examined from several points of view the general biological problem of the correlation between hereditarily conditioned traits of an organism and the influence of the environment. The central idea of the book was the belief that it was equally important for theory and for practical human undertakings to study the law-like regularity of heredity as well as the impact of various influences of the external environment on the organism. In a variety of examples Conklin showed the influence of the environment on individual development. He arrived at the conclusion that "variations are of two kinds, those which are caused by a

[12] *Ibid.*, p. 154.

different germinal constitution and are therefore inherited and those due to environmental differences which are not inherited."[13] By the noninherited influence of the environment, Conklin meant only its effect on the soma, which did not reach the sex cells. He did not regard the hereditary substance as immutable and cited proofs of the possibility of its change under the influence of external factors. That conclusion did not entail, however, admission of the inheritance of acquired characters. Conklin devoted a special part of the chapter "Influence of Environment" to this issue. He very clearly posed the central questions which needed answering: "Can peculiarities of the environment which influence the development of somatic characters so affect the germ cells that they will produce these somatic characters in the absence of the peculiar environment? Can the characteristics of a developed organism enter into its germ cells and be born again in the next generation?"[14] Considering this improbable on an *a priori* basis, Conklin nevertheless briefly discussed unsuccessful or subsequently refuted attempts to show experimentally the possibility of the influence of the soma on sex cells. He gave us the colorful expression: "the wooden legs do not run in families, although wooden heads do."[15]

A book by Aleksandr Petrovich Vladimirskii deserves a more thorough examination.[16] Very conscientiously and with scientific circumspection the author analyzed various indirect arguments and experimental data which supported the hypothesis of inheritance of acquired characters. Vladimirskii's own opinions appear on the first pages of his book. "It is necessary to assume only that . . . different new traits received by the organism during the course of its individual life will be transmitted by heredity to its children, and we very simply solve the question of the paths and methods of evolution."[17] From this remark it is apparent that Vladimirskii saw no difference between variation and evolution. He proposed that the direction of the evolutionary process was directly determined by the direction of changes which arose under the influence of the external environment. Vladimirskii also made no significant distinction between Lamarckian and Darwinian explanations of factors of evolution. He figured that both systems were founded only on suppositions, "and therefore it will be a matter of personal choice which supposition is accepted."[18] Vladimirskii's

[13] Edwin Grant Conklin, *Nasledstvennost' i sreda* [*Heredity and Environment*], trans. from the 5th English edition, Iu. A. Govseev, ed. and foreword M.M. Zavadovskii (Moscow-Leningrad: 1928), p. 75. [Passage follows Conklin, *Heredity and Environment in the Development of Men* (5th ed.; Princeton: Princeton University Press, 1923), p. 72.]

[14] *Ibid.*, p. 250. [*Ibid.*, p. 239.]

[15] *Ibid.*, p. 251 [*Ibid.*, p. 240.]

[16] Aleksandr Petrovich Vladimirskii, *Peredaiutsia li po nasledstvu priobretennye priznaki?* [*Are Acquired Characters Transmitted By Heredity?*] (Moscow-Leningrad: 1927), p. 184.

[17] *Ibid.*, p. 5.

[18] *Ibid.*, p. 28.

personal sympathies were unquestionably inclined toward a viewpoint close to Lamarckism, but he did not identify them with contemporary neo-Lamarckism. While declaring himself "a proponent of the basic significance of the environment in the process of evolution," Vladimirskii nevertheless regarded the views of Lamarckism as one-sided. In his opinion, adherents of Lamarckism, such as Kammerer, Smirnov, Vermel', and Kuzin, "who regard somatic induction as their central theme, strive to convince their opponents that this concept is already rigorously proven by the material facts available."[19] Vladimirskii believed that the problem of the transmission of acquired characters should encompass all inheritable properties of whatever origin. Among those properties and perhaps principal among them were those that were caused by an influence on the hereditary substance only, that is mutations. Vladimirskii was obviously not troubled by the fact that in the origin of mutations the traits of the parent organism were not altered. This means that in this case the "acquired trait" whose inheritance was liable to explanation was absent. Emil Guyénot, whose views are described later on (see chapter 11), clearly explained what confusions arise from such a broad interpretation of the concept of "inheritance of acquired characters."

Vladimirskii correctly believed that since the question of the inheritance of acquired characters could be resolved only by experimental means, the controversy between neo-Darwinians and neo-Lamarckians would remain unproductive as long as only indirect arguments were used. Even as decided an advocate of the inheritance of acquired characters as George Henslow admitted that this indirect path of argumentation was not as rigorous and exact as an experiment. This despite the fact that Henslow himself had collected evidence by direct observation of nature that he thought strongly suggested such transmission in plants.[20] All the same, Vladimirskii did not refuse to employ indirect arguments. He noted that "identical traits possessed by completely different plants are undoubtedly most easily understood as the result of the influence of the environment, i.e., as the result of adaptation to identical conditions." "The idea naturally suggests itself," Vladimirskii continued, "that here we have a matter of causal relationship, that . . . organisms which find themselves in new conditions change as a result and take on adaptive traits."[21] Here once more the results of the influence of the environment on the individual were equated with adaptation of a species to its surroundings. In fact, the ability to make individual adaptations does not presuppose the ability to transfer these adaptive changes to one's progeny. The fact that one is able in an experiment to reproduce this or that change by altering the conditions speaks only in support of the ability of the organism to change, and says nothing of the inheritability of these changes.

[19] *Ibid.*, p. 161.
[20] Henslow (n. 3).
[21] Vladimirskii (n. 16), pp. 16–17.

Among other examples of indirect arguments in support of the inheritance of acquired traits, Vladimirskii cited the development of callouses on the anterior limbs of the warthog and noted that "R. Semon, in his book on the inheritance of acquired traits (1912), regards this fact as a classic example of the inheritance of functional changes."[22] Vladimirskii also spoke of the reduction of the eyes in crustaceans in the dark. The deeper a given species lives, the greater that reduction. He wrote, "Here it is as if nature is indicating the path by which gradual reduction of the organ came about."[23] In this he did not pay attention to two logically conceivable possibilities: (1) underdevelopment of the eye as the result of disuse and (2) the elimination of a variation which has become useless to the organism. Vladimirskii noted in another context that "the origin of various adaptations is *also* easily explained by the Darwinian theory of natural selection."[24] One must not be surprised by the "also." For nearly seventy years after the publication of the *Origin of the Species* Darwin's theory of the origin of adaptive changes via natural selection was mentioned only as one of the possible explanations of the evolutionary process, and at that it held second place to the Lamarckian hypothesis of direct adaptation.

Despite all this, in its day Vladimirskii's book played an unquestionably positive role. The fourth chapter, "Attempts at a direct proof of somatic induction," deserves special attention. The fastidious discussion of experiments and careful evaluation of them is of undeniable merit. In particular, Vladimirskii reviewed experiments on the transplantation of gonads in mammals, birds, amphibians, and butterflies (these experiments will be spoken of in more detail in chapter 18) and concluded, "It must be admitted that all attempts to reveal somatic induction by transplantation of gonads came to nothing."[25] Vladimirskii likewise evaluated the results of attempts to obtain graft hybrids in plants. "Here as well, the influence of the foreign soma was in no way manifested."[26] Summarizing the data in the literature and his own experimental data on somatic induction, Vladimirskii wrote, "I do not at all want to insist that somatic induction actually takes place and that it will be proven sometime. The experiments to date are far from proving the point." Vladimirskii regarded as unfounded the stance taken by Kammerer and supported by Bernhard Dürken that old traits normally inherent in the organism cannot influence the sex cells but

[22] *Ibid.*, p. 21.
[23] *Ibid.*, p. 22.
[24] *Ibid.*, p. 28.
[25] *Ibid.*, p. 74
[26] *Ibid.*, p. 76

that only "newly acquired, still active, imbalanced [uncorrelated?—N.H.] traits" are capable of such an effect. Vladimirskii commented with good-natured irony, "Somehow in such a hypotheses there is little internal logic."[27]

Summing up the experiments meant to demonstrate the inheritance of mechanical injuries, Vladimirskii wrote that they "in no way substantiate the inheritance of acquired traits."[28] He drew the same conclusion regarding Michael Frederic Guyer and E.A. Smith's research on chemical injuries to the crystalline lens, since their results had been refuted. Concerning the question of the inheritance of functional changes, Vladimirskii remarked that "there are almost no precise, systematic, long-term experiments on this matter."[29] Vladimirskii completely and correctly evaluated the results of William Lawrence Tower's temperature experiments on the Colorado beetle, which had long been considered proof of the inheritance of acquired traits. "The inheritable changes, received under the influence of external factors, cannot be attributed to somatic induction because in this example the soma of the parents does not experience any visible changes.... [Conversely,] when the parents themselves change, their progeny remain normal."[30]

Calmly and without bias Vladimirskii examined the pros and cons of Kammerer's assorted experiments, which had been subjected to criticism many times. Some of these experiments he regarded as convincing and others as requiring more precise reexamination. Vladimirskii reviewed experiments by Dürken and Leonora Brecher as well as his own on the influence of background color on the coloration of butterflies. He could not decide how to explain the change of coloration in progeny. He thought it could be attributed to the inheritance of changes acquired by the parents or to the selection of a race which possessed the pertinent hereditary traits.

To the question posed in the title of his book *Are Acquired Characters Inherited?*, Vladimirskii answered in the affirmative though the entire content of the book essentially contradicts this conclusion. In fact, he had in mind principally the results of the impact of external conditions on the germ-plasm, that is, mutations. He admitted that the possibility of adaptive changes in the germ-plasm under the influence of changes in the soma remained unproven.

Three years later at the Fourth Congress of Zoologists, Anatomists, and Histologists Vladimirskii expressed himself still more cautiously. He criticized the experiments of Dürken which supposedly demonstrated the inheritance of the results of coloration changes in cabbage butterfly pupae

[27] *Ibid.*, p. 78.
[28] *Ibid.*, p. 85.
[29] *Ibid.*, p. 92.
[30] *Ibid.*, p. 105.

under the influence of flower color. Referring to new data from his own experiments on cabbage moth pupae, Vladimirskii showed that "the inheritance of pupal coloration, which appeared to be induced by external factors, was actually caused by an unrecognized selection during which various covert hereditary races in the population became evident."[31] He refused to join those who strove to disassociate from Lamarckism "that part which corresponds to a earlier period of biology, namely, the idea of inheritance by a form of somatic induction." Vladimirskii proposed to define Lamarckism as that doctrine which emphasized the importance for evolution of external influences in general, to subsume such "Lamarckism" under Darwinism, and by so doing to follow the "fundamental direction of contemporary evolutionary thought."[32]

Ivan Mikhaslovich Poliakov came out against this proposal. He correctly noted that Vladimirskii confounded the problem of the transmission of acquired traits with the influence of the environment "in general," which included the origin of mutations by external influences. Poliakov likewise rejected any eclectic attempts to combine Lamarckism and Darwinism into one system.[33]

The unjustifiably broad interpretation of the concept of "acquired traits," including changes which depended on the direct influence of the environment on the germ-plasm, was at one time rather widespread. In a book devoted to theories of evolution Yves Delage and Marie Goldsmith considered two possible interpretations of this concept. According to the narrower interpretation, which Weismann adhered to, one should consider an acquired trait only that which could not be traced to the egg or spermatozoid. To characterize the broader interpretation, these authors referred to the opinion of Thomas Harrison Montgomery, who wrote, "In the facts of transformation of species . . . we have an indubitable case of the hereditable transmission of characters acquired in the history of the race. For each step in transformation is the inheritance of a new character that has become acquired."[34] Delage and Goldsmith believed that "all variations are therefore acquired, and we are not justified in designating

[31] Aleksandr Petrovich Vladimirskii, "Über die Vererbung experimentell erzeugter Färbung von Puppen der Kohlmotte Plutella maculipennis," *Biol. Zbl.*, 1928, *48:* 739–752.

[32] A.P. Zladimirskii, "Lamarkizm, ego itogi i novyi zadachi" ["Lamarckism, Its Conclusions and New Problems"], *Tr. IV Vses. s'ezda zool. anat. i gistol.* [*Transactions of the IV All-Union Congress of Zoologists, Anatomists, and Histologists*] (Kiev-Kharkov: 1931), pp. 33–35.

[33] Ivan Mikhailovich Poliakov, "Metodologiia lamarkizma" ["Methodology of Lamarckism"], *Tr. IV Vses. s'ezda zool., anat i gistol.* [*Transactions of the IV All-Union Congress of Zoologists, Anatomists, and Histologists*], (Kiev-Kharkov: 1931), pp. 40–41.

[34] Thomas Harrison Montgomery, *The Analysis of Racial Descent in Animals* (New York: Henry Holt & Co., 1906), p. 150. [Cited in Yves Delage and Marie Goldsmith, *The Theories of Evolution* (New York: B.W. Huebsch, 1913), p. 193.]

exclusively as acquired those which appear in the later period of the individual's life,"[35] that is, for changes which originated as the result of influences on the soma. To characterize the lack of appropriateness of the concept by which Delage and Goldsmith operated, one may cite their reference to the experiments of Paul Bert on the action of salt water on Daphnia. The Daphnia themselves died in a solution of 1.5% salt, but their eggs remained viable and gave offspring which could tolerate such a concentration of salt. Delage and Goldsmith wrote of this example: "[Alpheus Spring] Packard, a Lamarckian, . . . sees in it evidence of the heritability of a modification, but J. Arthur Thomson, a Weismannian, regards it merely as an instance of the direct modification of the germ cells or of the embryos."[36] Delage and Goldsmith did not notice the crucial fact that since the Daphnia subjected to the action of salt die, they had not acquired the trait of salt tolerance, and therefore tolerance in their progeny could not bear witness to the inheritance of an acquired trait.

[35] Delage and Goldsmith (n. 34), p. 194.
[36] *Ibid.*, p. 198.

CHAPTER 9

Discussions in the Soviet Union Concerning the Inheritance of Acquired Characters: 1920s

During the mid-twenties in the Soviet Union biologists, philosophers, and sociologists held animated discussions on problems in general biology which encompassed an important methodological principle. In 1925 Friedrich Engels's book, *Dialectics of Nature,* was published for the first time, appearing simultaneously in Russian and German.[1] Its intense study by wide circles of the Soviet intelligentsia raised many questions concerning the discovery of the laws of dialectical materialism in the phenomena of nature. These included particularly phenomena characterizing the structure, functions, variability, inheritance, and development (ontogenetic and phylogenetic) of living organisms. The participants in these discussions naturally could not avoid the confrontation which was being actively discussed in the international scientific and popular literature—that of Darwinism versus Lamarckism. By this time, each of these alternatives in biological thought had fractionated into several, at times fundamentally differing, positions. The basic problem facing the disputants amounted to determining which position most closely corresponded to the methodology of dialectical materialism. It was quite natural that one of the specific, and yet fundamental, questions considered was that of the inheritance of acquired characters.

In order to characterize the discussion we will present the statements of the proponents and opponents of the inheritance of acquired traits, as well as the attempts to reconcile eclectically the opposing views, in which eclecticism was passed off as a dialectical unity of opposites. Boris Mikhailovich Zavadovskii in particualr held the latter position, although on the whole he leaned more toward the Darwinian than the Lamarckian concept of evolution.[2] Citing the available experimental data concerning the inheritance of acquired traits, he noted that they testified in some instances in favor of,

[1] Friedrich Engels, *Dialektika prirody* [*Dialectics of Nature*], *Arkhiv K. Marksa i F. Engel'sa* [*Archive of K. Marks and F. Engels*] Bk. 2 (Moscow-Leningrad: 1925), p. 501.
[2] Boris Mikhailovich Zavadovskii "Predislovie" ["Preface"], in E.S. Smirnov, Iu. M. Vermel', and B.S.Kuzin, *Ocherki po teorii evoliutsii* [*Essays On the Theory of Evolution*] (Moscow: 1924).

but in the majority of cases against, the transmission of such characters. During these years the Timiriazev Institute was founded. Some of its researchers espoused the inheritance of acquired characters.

Certain physicians also held Lamarckian views. Among them was Solomon Grigor'evich Levit, who organized a circle of medical materialists within the medical faculty of the first Moscow University. Levit's Lamarckian views, stemming from the early period of his career, are reflected in a lecture read in 1924 for the circle of medical materialists and published two years later.[3,4]

In 1926 the Biological Laboratory was founded for the purpose of studying the inheritance of acquired characters. Here investigators set up tests to verify Kammerer's original experiments which maintained the heritability of changes in the salamander's coloration under the influence of a colored background. This work did not yield positive results, judging by the fact that the findings were not published anywhere.

In the same year, 1926, the Timiriazev Institute published a collection of discussions, *Preformation or Epigenesis?*, devoted mainly to the problem of the inheritance of acquired traits.[5] E.S. Smirnov and N.D. Leonov[6] and B.S. Kuzin[7] defended Lamarckian concepts in their articles. They constructed arguments on the basis of *a priori* assumptions drawn from mechanics and energetics. At the same time they reported without critical comment the factual material for and against the assertion of the inheritance of acquired changes. All experiments which did not confirm the inheritance of acquired traits were rejected without any serious discussion whatsoever. Only the article by Theodosius Dobzhansky, who was then a research fellow at the laboratory of Yurii A. Filipchenko, handled the question with the proper objectivity. Dobzhansky cited in particular the fact that common breeding practices did not employ Lamarckian principles and yet the successes of selection were great and indisputable.[8] Dobzhansky correctly attributed great significance to this testimony from

[3] This circle propagandized dialectical materialism among doctors and students.

[4] Solomon Grigor'evich Levit. In *Meditsina i dialekticheskii materializm* [*Medicine and Dialectical Materialism*] Transactions of the Circle of Physician-Materialists for the year 1924-25 (Moscow: 1926), pp. 15-32.

[5] This collection provided the opportunity to compare the strength of arguments for and against such inheritance.

[6] Eugenii Sergeevich Smirnov and N.D. Leonov, "Preformizm ili epigenezis?" ["Preformation or Epigenesis?"] in the collection *Preformizm ili epigenezis?* [*Preformation or Epigenesis?*] (Vologda: 1926), pp. 1-24.

[7] Boris Sergeevich Kuzin, "Krizis preformizma" ["The Crisis of Preformationism"], in the collection *Preformizm ili epigenezis?*, pp. 51-61.

[8] Theodosius Dobzhansky, "K voprosu o nasledovanii priobretennykh priznakov" ["On the Question of the Inheritance of Acquired Traits"], in the collection *Preformizm ili epigenezis?*, pp. 27-47.

common practice. In his article he criticized Smirnov and Leonov's article included in the same collection and a book by Smirnov, Vermel', and Kuzin. Above all, he noted that these authors lacked clarity in posing the very question under investigation. They confused two fundamentally different phenomena—true changes in the hereditary disposition versus false inheritance and long-term modifications. Smirnov and Leonov suggested that it constituted sufficient evidence of the inheritance of acquired characteristics "if one can succeed in showing that the change occurring in the organism while under the influence of external factors is transmitted to the next generation even when the latter is nurtured once again under normal conditions."[9] Dobzhansky said that this might seem acceptable only at first glance.

Among the arguments cited in favor of the inheritance of acquired characters we will deal first with instances of false inheritance. Examples of this would be the transmission of infectious diseases from the mother to the fetus and the penetration of dye received in food into the cytoplasm of the egg with the ensuing coloration of the offspring. Dobzhansky asked what exactly was inherited in the transmission of traits from parents to children. He gave the example of two varieties of the Chinese primrose, one having red flowers the other white flowers at room temperature, while at an elevated temperature (35°C) both varieties produce white flowers. Upon transfer once again to normal temperature the "white" variety remains white, while the "red" again forms red flowers. He also gave the example of the "abnormal abdomen" mutation in the fruitfly, that is, the improper placement of stripes. This characteristic appears in larvae raised on moist food, but when given dry food, the mutants do not differ from normal flies. From these two examples Dobzhansky concluded that it was not the character of the organism which was inherited but a norm of reaction to one or another environmental condition. A trait might easily change while the norm of reaction remained very stable. Even maintaining the mutant flies on dry food for dozens of generations (Morgan's experiment), "abnormal abdomen" did not appear, but it immediately appeared in the next generation if the offspring of such flies were transferred to moist food. Therefore when considering the inheritance of acquired traits, it was necessary to focus not on the inheritance of traits altered under the influence of an external agent but on the inheritance of a norm of reaction altered by this influence. Attempts to change the norm of reaction, however, had not been successful.

Dobzhansky suggested strictly differentiating hereditary alterations from long-term modifications. Morphological variations which were induced in Daphnia by malnutrition (Woltereck's experiment) and the variation

[9] Smirnov and Leonov (n. 6), p. 10.

in coloration of the chrysalis of the cabbage butterfly kept under orange light (experiments of Dürken and others) persisted to a gradually diminishing degree through a number of generations. These phenomena could be explained by the supposition that the eggs penetrated by substances formed under unusual environmental influences in the parent organisms.

Further on in his discussion Dobzhansky concentrated on the experiments of Paul Kammerer. He considered most questionable the results of Kammerer's experiments with the midwife toad in which, under the influence of an elevated temperature, the reproductive instinct (emergence onto dry land for spawning) changed and pigmented nuptial callouses appeared on the big toes of the forelimbs. These new traits were subsequently transmitted through a number of generations in accordance with Mendel's laws without attenuation. Since these data contradicted all that was known to genetics concerning the laws of inheritance, Dobzhansky offered the suggestion that from the beginning Kammerer was dealing with heterozygous material and observed not the inheritance of acquired traits but the segregation of traits.

Also doubtful were the results of Kammerer's experiments with the fire salamander which changed coloration under the influence of a colored background and which transmitted the induced alterations. These experiments were more questionable considering the fact that Curt Herbst's attempts at verification did not corroborate Kammerer's results. Smirnov and Leonov reported that Bulendzher had been successful in repeating Kammerer's experiment and obtaining a change in coloration in the salamander, but in fact, Bulendzher's results were never verified. "But we consider," wrote Smirnov and Leonov, "that if one half of the experiment was verified then we may rely with some confidence on the other half."[10] "This assertion," Dobzhansky rightly noted, "can scarcely appear warranted to anyone but the proponents of the assertion."[11] In fact, in order to be convinced of the veracity of Kammerer's basic conclusion, it was far more important to check not the fact of the appearance of changes, which did not represent anything inconceivable, but precisely the assertion that such changes were inherited. Dobzhansky preferred to interpret the results of Kammerer's experiments with salamanders, if confirmed, as long-term modifications. Kammerer himself noted that the induced traits became less noticeable after several generations and that upon crossing altered individuals with normal ones, the progeny exhibited intermediate traits of coloring and did not display Mendelian segregation.

M.F. Guyer and E.A. Smith performed experiments which seemed to confirm the inheritance of defects in the crystalline lens in rabbits when the parents were exposed to anti-crystalline lens serum. According to Smirnov

[10] *Ibid.*, p. 14.

[11] Dobzhansky (n. 8), p. 38.

and Leonov, who ignored refutation by other authors, these experiments "fully retain their validity for epigenesis."[12] Dobzhansky wrote about Smirnov and Leonov's conclusion, "One must assume that the substances secreted by the injured eye reached the 'hereditary factors' of the eye in the sex cells and had the same disruptive effect on these factors. If that is true, then it inevitably follows that the eye of the animal and the hereditary factor of this eye in the germ cell have, if not the same physical structure, then at least a very similar chemical composition. Ideas of a similar sort concerning the nature of the inheritance of rudiments are, of course, the crudest preformationist notions and one can only be astonished that the 'epigenesists' consider them acceptable."[13] Dobzhansky considered one of the arguments against the inheritance of acquired characters to be the law of the "purity of gametes," which predicts the absence of the mutual influence of allelomorphic genes and which, according to Dobzhansky, was one of the most firmly established facts of biology.

Dobzhansky, as well as the "epigenesists" with whom he carried on the debate, recognized the primacy of the question: what causes the emergence of heritable changes? but he was forced to admit that the causes were still unknown.[14] One must keep in mind that these views were written before the publication of the experiments in which Hermann J. Muller obtained mutations in Drosophilia by means of X-rays. "However sorry this state of affairs," concluded Dobzhansky, "it would be pointless because of our ignorance of the true principles of mutant changes to accept the utterly unfounded possibility of the inheritance of acquired characters."[15]

In fact, not only did geneticists believe genes to be capable of change under the influence of environmental action, but they themselves attempted to induce mutations by means of such influences. In a speech at the opening of the Fourth All-Union Congress of Zoologists, Anatomists, and Histologists (Kiev, 1930) Nikolai Konstantinovich Kol'tsov recalled his speech of 1916 in which he had said, "We should, by means of a severe shock to the germ cells, change their hereditary organization and from among those emerging forms which are hereditarily stable . . . choose the most viable. . . . We will not have long to wait till man at his own will can create new life forms."[16] In the same speech Kol'tsov reported that after

[12] Smirnov and Leonov (n. 6), p. 15.

[13] Dobzhansky (n. 8), p. 39.

[14] During the preceding year in *Vestnik rentgenologii i radiologii* [*Radiology and Roentgenology Herald*] an article was published by G.A. Nadson and G.S. Filippov, who showed for the first time the effect of x-rays on saprophytic fungus (see n. 18), but obviously it was not known to Dobzhansky.

[15] Dobzhansky (n. 8), p. 46.

[16] Nikolai Konstantinovich Kol'tsov, "Ob eksperimental'nom poluchenii mutatsii" ["On Obtaining Experimental Mutations"], in the collection *Organizatsiia kletki* [*Cell organization*] (Moscow-Leningrad: 1936), p. 497.

Nikolai Konstantinovich Kol'tsov
(1872-1940)

the organization in 1917–18 of the Institute of Experimental Biology he had instructed Dmitrii Dmitrevich Romashov to carry out a program of radiation of Drosophilia. "When we had obtained a few seemingly positive results, we were cautious in their interpretation and did not publish them. The danger of an incorrect interpretation of the results from material that had been insufficiently investigated by geneticists was quite obvious. The mistakes of Kammerer and other Lamarckians warned against hasty conclusions."[17] In 1925 Georgii Adamovich Nadson and Georgii Sergeevich Philipov reported obtaining changes in a saprophytic fungus by means of X-rays, but their work remained unnoticed at that time.[18]

In 1926 a paper by Aleksandr Sergeevich Serebrovskii, which had been read in the Natural and Exact Sciences Section of the Communist

[17] *Ibid.*, p. 497.

[18] Georgii Adamovich Nadson and Georgii Sergeevich Filippov, "O vliianii rentgenovskikh luchei na polovoi protsess i obrazovanie mutantov u nizshikh gribov (Mucoraceae)" ["On the Effect of Roentgen Rays on the Sexual Process and Formation of Mutations in Lower Fungi (Mucoraceae)"], *Vestn. rentgenol. i radiol.* [*Radiology and Roentgenology Herald*], 1925, no. 3, rpt. in the collection *Klassiki sovetskoi genetiki* [*Classics of Soviet Genetics*] (Leningrad: 1968), pp. 120–124.

Academy, was published in the journal *Under the Banner of Marxism.* While admitting that geneticists were not yet able to influence the process of mutation, Serebrovskii noted, "From this, of course, it does not follow that we will never find a means to penetrate the protoplasm without damaging it and to act upon the chromosomes. Attempts by Muller, one of the most brilliant members of the Morgan school, to affect the chromosomes by means of X-rays are the best evidence of this. They have already yielded certain results."[19]

After comparing the theses of the "naive point of view which insisted that inherited elements could be easily changed," and its antitheses, "which insisted . . . on the impossibility of their change," Serebrovskii came to the conclusion that "we are now approaching a syntheses which proclaims that in all probability genes, too, can be changed, if only we can learn how and upon what to act."[20]

In that same year, 1926, the Society of Biological Materialists was organized. At a session of this society Smirnov gave a paper entitled "Problems of the hereditary influence of the environment and evolution." In this presentation he again made uncertain assertions concerning the possibility of inducing changes in the germ cells by an influence from the altered soma. Such changes, he claimed, led to very similar alterations in the progeny which developed from the germ cells. Smirnov dealt mainly with the experiments of Kammerer, who attended the session. Any objections which had been made to Kammerer's work he merely mentioned in passing. Assuming the geneticists' viewpoint, Smirnov stated that "the acceptance of 'internal causes' for heritable changes leads to the acceptance of autogenesis, that is, of evolution based on internal altering forces obviously nonmaterialistic in character."[21] The presentation also touched on the question of an explanation for the emergence of adaptations. "We are often asked, 'How can we explain the origin of appropriate adaptation . . . ?' First of all one must point how crudely teleological such a question is."[22]

S.G. Levit, who took part in the debates, noted in this connection, "To sidestep the question of appropriate adaptations—the correlation of organization and function—by saying that this is a teleological question, is an intentional misrepresentation. . . . What else except natural selection can be used to explain the presence of existing adaptations."[23]

[19] Alexandr Sergeevich Serebrovskii, *Pod znamenem marksizma* [*Under the Banner of Marxism*], 1926, *no. 3:* 105.

[20] *Ibid.*, p. 108.

[21] *Arkhiv AN SSSR* [*Archive of the Soviet Academy of Science*], folio 350, opus la, no. 73, p. 2.

[22] *Ibid.*, p. 19.

[23] *Ibid.*, p. 26.

In the same symposium Serebrovsky devoted his presentation to a criticism of Kammerer's experiments that Smirnov had cited in his paper. He noted that the critics of Kammerer "pointed out that the material with which Kammerer worked was material taken from nature. No geneticist works with such material . . . they then showed that Kammerer was not scrupulous in his manipulation of data, allowing an enormous share of subjectivity." Using the example of the midwife toad, Serebrovskii paid special attention to the question of the inheritance of instincts which were altered by external influences. "Contemporary geneticists," said Serebrovskii, "serious geneticists, once they established that a given phenomenon follows Mendelian laws, do not act at all as Kammerer did. . . . I do not accuse Dr. Kammerer, for when he did his work, Mendelism was in a very undeveloped state. . . . Now, when we wish to determine whether a given phenomenon follows Mendelian laws, we test it by performing backcrosses and only then do we venture to say that we have obtained a Mendelian relationship."[24] Sergei S. Chetverikov also sharply criticized the Lamarckians' anti-genetics presentations.[25]

Smirnov's presentation and the debate concerning it were not published. A year later a pamphlet appeared which contained Smirnov's uncritical elucidation of the data available in the literature that concerned the inheritance of acquired characters.[26] Max L. Levin severely criticized both this pamphlet and an interesting booklet written from a Lamarckian point of view by Pavel A. Novikov.[27] In particular, Levin used documentation to refute the claim that Ivan Petrovich Pavlov was a supporter of the inheritance of acquired forms of behavior.[28]

Smirnov published a paper in the *Communist Academy Herald* defending the concept of the inheritance of acquired characters. He based his conclusions only upon peripheral arguments and upon unverified and methodologically unsuitable experimental data. Evidence which might speak for heritable changes obtained through indirect influences on the sex cells he mistook for evidence of somatic induction. Smirnov devoted much of his presentation to the central idea of Mechanistic-Lamarckism—the assumption that changes in the somatic portions of the organism give rise to corresponding changes in the sex cells. Smirnov tried to find a hypothetical explanation for this correspondence. He favored the suggestion that

[24] *Ibid.*, pp. 30–31.

[25] *Ibid.*, p. 33.

[26] Eugenii Sergeevich Smirnov, *Problema nasledovaniia priobretennykh priznakov. Kriticheskii obzor literatury* [*The Problem of the Inheritance of Acquired Traits: A Critical Review of the Literature*] (Moscow: 1927), 28 pages.

[27] Pavel Aleksandrovich Novikov, *Teoriia epigeneza v biologii. Istoriko-sistematicheskii ocherk* [*The Theory of Epigenesis in Biology: An Historic-Systematic Essay*] (Moscow: 1927).

[28] *Pravda* [*Truth*], 1927, *no. 106.* For further details see chapter 17.

Sergei Sergeevich Chetverikov
(1880–1959)

the soma influenced the sex cells by means of hormones. "If . . . as the result of a change in the environment, a particular organ is forced to exert itself, then this exertion will cause an unusual configuration in the hormones in the given organ. These hormones then enter into the sex cells and . . . in the next generation, by virtue of their specificity, give rise to the same results in the parent generation. These conditions nicely explain induced inheritance."[29] Assuming the existence of hormones, which could be produced in any part of the organism, and of autocatalysts responsible for the formation of these hormones, Smirnov, who was not a physiologist nor biochemist, but a systematic entomologist, believed it possible to derive from these an "excellent solution to the problem of induced inheritance of acquired traits."[30]

Levin was correct in saying that Smirnov's presumed universal explanation of the inheritance of acquired characters was indefensible. He also

[29] Eugenii Sergeevich Smirnov, "Novye dannye o nasledstvennom vliianii sredy i sovremennyi lamarkizm" ["New Data Concerning an Inherited Environmental Effect and Contemporary Lamarckism"], *Vestn. Kom. akademii* [*Communications of the Communist Academy*], 1928, Bk. 25: 192.

[30] *Ibid.*, p. 194.

noted the fact that "the very process of inheritance of such traits has not yet been proven." "Why," Levin asked, "should the transmission of acquired somatic traits become more understandable with the help of autocatalysts about which we have no information? . . . In my opinion, we have here only words. You would be better off first establishing whether specific autocatalysts indeed exist. . . . Everything that I have just said applies to various hormonal theories of inheritance as well. . . . Premature generalizations which attempt to take in too much may in the first place hinder the very study of internal secretions."[31]

Mikhail Mikhailovich Mestergazi
(1884-1954)

A paper delivered by Mikhail Mikhailovich Mestergazi to the Society of Biological Materialists summed up the discussions on topics of general biology which had unfolded in the Soviet Union during the mid-twenties. The speaker concisely characterized evolutionary concepts which had taken shape up to that time. He emphasized that "one often had to deal with assertions which, from the point of view of the materialist discussing the problem of evolution, seem to require acceptance of the inheritance of acquired traits."

[31] *Ibid.*, pp. 203-204.

Mestergazi compared the views of the preformationists and epigenesists, that is, auto- and ectogenesists on one hand and the views of the opponents and proponents of the inheritance of acquired characters on the other. He strongly objected to the opinions of Lamarckians, who "imply that everyone who defends epigenetic views, that is, who admits the influence of external factors in heredity, by implication aligns himself with the traditional belief in the inheritance of acquired characters. This, of course, is actually not the case."[32] Mestergazi noted that in the middle of the nineteenth century no one except von Baer denied the inheritance of acquired traits and that Darwin was no exception. He drew the important conclusion that although "Darwin himself accepted the inheritance of acquired traits," nonetheless, "this question did not at all form an essential element in the overall structure of Darwinism."[33]

In the discussions about the inheritance of acquired traits, as Mestergazi correctly pointed out, the supporters of such inheritance, "wittingly or unwittingly misrepresented the facts. An acceptance of the physicochemical factors which underlie hereditary variability or an acceptance even of the possibility of artificially inducing such changes is not at all equivalent to a recognition of the hereditary transmission of changes that occur in the organism under the influence of the environment or exercise. Acknowledging the ectogenetic mutability of the determinants of hereditary characters places us among the ranks of the epigenesists, who are convinced of the possibility of actively interfering in this mutability, and at the same time allows us to break conclusively with Lamarckism."[34]

In the twenties the discussions of these principles in biology led to the publication of interesting popular-science books which showed convincingly the lack of proof and the invalidity of methods of neo-Lamarckism. Among these books we should mention those of Israel I. Agol,[35] I.M. Poliakov,[36] and especially Eugenii Aleksandrovich Finkel'shtein.[37] These authors polemicized against the proponents of Mechanistic-Lamarckism. Proceeding from the fact that experimental verification of the inheritance of acquired traits had led to negative results, they came to the well-founded

[32] Mikhail Mikhailovich Mestergazi, "Epigenezis i genetika" ["Epigenesis and Genetics"], *Vestn. Kom. akademii* [*Communications of the Communist Academy*], 1927, Bk 19: 187.

[33] *Ibid.*, p. 189.

[34] *Ibid.*, pp. 192-193.

[35] Israel Agol, *Dialekticheskii materializm i evoliutsionnaia teoriia* [*Dialectical Materialism and Evolutionary Theory*] (Moscow: 1927). Cited according to E.A. Finkel'shtein (see n. 37).

[36] Ivan Mikhailovich Poliakov, *Sovremennaia evoliutsionnaia teoriia. Populiarnyi ocherk* [*Contemporary Evolutionary Theory: A Popular Essay*] (Kharkov: 1928).

[37] Eugenii Aleksandrovich Finkel'shtein, *Zhizn'kak dialekticheskii protsess* [*Life as a Dialectical Process*] (Kharkov: 1928).

conclusion that it was not Lamarckism but Darwinism that brought evolution into harmony with a dialectical materialistic view of nature. Lamarckism inevitably leads to an acceptance of immanent teleology, whereas Darwinism holds that mutability of the germ-plasm is in itself inadequate for evolution, that natural selection is required.

CHAPTER 10

Darwinians and Anti-Darwinians on the Inheritance of Acquired Traits

Alexandr Sergeevich Serebrovskii continued the discussion which was the subject of the previous chapter in an excellent but unjustly forgotten article that appeared in the then newly published scientific-philosophic journal of the Communist Academy.[1] He specially noted the lack of correspondence between the extraordinary poverty and inconclusiveness of the factual material upon which Lamarckians based their deductions and the wide dissemination of their views, especially among non-specialists.[2]

Serebrovskii drew attention to the fact that Lamarckians considered the principles of the phylogenetic history of the organic world and the principles of physiology to be one and the same; they saw no qualitative difference between the phylogenetic process of the evolution of species and the changes in individuals due to the direct influence of external conditions or to the intensity of functioning organs.

The qualitative uniqueness of the evolutionary process, which does not permit it to be reduced to the physiological phenomena of individual variation, consists in the fact that it does not have to do with separate individuals, the interactions among which make no difference for the physiological processes going on inside them. In contrast the aggregate of individuals reacts to changes in its environment precisely as an aggregate, that is, according to the laws of probability. Serebrovskii considered it a great legacy of Darwin that he "was not satisfied with attempts at purely physiological explanations of the evolutionary process," as were his predecessors Lamarck and Geoffroy Saint-Hilaire. Instead, he "introduced natural selection as the chief factor."[3]

[1] The questions examined by Serebrovskii were also illuminated in an interesting book by the talented popularizer Mestergazi, in which the latter engaged in polemics with mechanico-Lamarckists. In the philosophical debates of those years mechanicism was seen as the principle opponent of dialectical materialism. See Mikhail Mikhailovich Mestergazi, *Osnovnye problemy organicheskoi evoliutsii* [*Basic Problems of Organic Evolution*] (Moscow: 1930).

[2] Alexander Sergeevich Serebrovksii, "Opyt kachestvennoi kharakteristiki protesessa organicheskoi evoliutsii" ["Experiment on the Qualitative Characterization of the Process of Organic Evolution"], *Estestvozn. i marksizm* [*Natural Science and Marxism*], 1929, *no. 2:* 53.

[3] *Ibid.*, p. 57.

Alexandr Sergeevich Serebrovskii
(1892-1948)

To help demonstrate the fact that the development of protective adaptations in plants and animals could not be the result of the direct influence of their enemies, Serebrovskii cited the phenomenon of mimicry. In particular, he gave the well-known example of the similarity of the wings of the Kallima butterfly to the leaves of certain trees. Serebrovskii wrote, "There is no doubt that the development of such an insect in the process of phylogenesis is in some way related to the existence in nature of an eye which looks at the butterfly. The evolution of form and coloration of the mimicking butterfly and of the eye which looks at it must develop in conjunction with one another. We are perfectly right to say that this eye influences the form and coloration of the butterfly. . . . Yet it is easy to show that this influence is qualitatively of a completely different order than a physiological influence. . . . Here we have an influence without any sort of contact. In fact, if the possessor of this eye sees the butterfly, he will capture it. Only those butterflies which the eye does not notice, that is, does not distinguish from leaves, will remain alive. If we consider the modern Kallima, we recognize that the entire line of its predecessors consisted of those butterflies which never came into contact with the possessor of the eye." [4] In order to designate this qualitatively unique relationship, which is

[4] *Ibid.*, p. 59.

not reducible to a physiological influence but is the result of natural selection, Serebrovskii proposed the term "indirect causal relationship." Despite the lack of success of the term itself, we cannot help but notice that it precisely expresses the essence of the matter.

Another of Serebrovskii's examples had to do with the "indirect" mutual interaction of insects that feed on nectar and the plants that they pollinate. In the former there develop adaptations for extracting nectar from the deeplying parts of the blossom, and in the latter, adaptations which guarantee the sprinkling of the insect with pollen and its transfer to the pistil of another blossom. "It would be absurd to imagine," wrote Serebrovksii, "that this remarkable system of levers in the stamens of the sage is the result of the physiological pressure of the head of the insect on the stamen." [5]

Further on Serebrovskii spoke of the development of epidermal protective structures in Devonian armored fish and the powerful dental armament of their contemporaries, the sharks. He noted that, "Devonian fish, those bearers of armor, . . . comprised an unbroken line of generations of individuals whom none could bite into, . . . in any case the armor did not develop because the skin of the fish was "exercised" to render resistance to the teeth of sharks." [6] On the other hand, "strong armor eliminated from the arena of life those predators which could not bite through [their prey], and only the sufficiently armed predators survived." [7]

Serebrovskii illustrated the same idea in an example drawn from a completely different sphere. "Just as in studying Devonian fish we rejected the explanation that their armor developed under the influence of a physiological irritation of the skin by shark teeth, we must likewise reject the explanation that warship armor thickened due to the impact of enemy artillery shells." [8]

Serebrovskii also used the example of worker bees, which possess special structures for the collection of honey and pollen, to demonstrate the irreducibility of the evolutionary process to the process of individual changes. One might suppose, as Lamarckians did, that changes in the tarsi and the proboscis of workers, which render these parts better adapted for their special tasks, arose as the result of "exercise" and the transmission to the progeny of the results of this exercise. It is well known, however, that workers do not reproduce, and that those individuals which, among bees, assure the inheritance of any traits—queens and drones—do not "get exercised" in the collection of honey and pollen and are thus devoid of adaptations essential for this function.

[5] *Ibid.*, p. 60.
[6] *Ibid.*, p. 61.
[7] *Ibid.*, p. 62.
[8] *Ibid.*, p. 66.

Lamarckians continued to insist on their views despite criticism which showed that they relied upon unconvincing experiments to defend the inheritance of acquired traits. Unjustifiably, they rejected the value of the synthesis between evolutionary theory and genetics. Smirnov, in particular, persisted in this vein in an article in which he attempted to examine the problems of genetics from a Lamarckian point of view. Once again he enlisted as supporting arguments the temperature experiments of Brecher and Dürken and the experiments of J.W. Heslop Harrison and F.C. Garrett on the influence of salts of metals—this despite the fact that it had already been shown that these investigations were unsound demonstrations of somatic induction.[9]

In reply to Smirnov's assertions, Nikolai Petrovich Dubinin, at that time an assistant to Serebrovksii at the Zoological Institute, published an article in the same journal. In summing up his discussion of the scientific status of genetics with respect to evolutionary theory, Dubinin came to the following conclusion: "In the methodological domain Lamarckism is a typical mechanistic theory. Its concepts of inheritable variation and the dependence of that variation on the influence of the soma and external conditions of the life of the organism are false to the roots (they disregard the qualitative uniqueness of the genotype and the phenotype and confound them)." Dubinin noted that Lamarckians misunderstood the uniqueness in the evolutionary process, the principles of which are qualitatively different from those of individual phenotypic variations. In this respect Lamarckians continued to identify the physiological phenomena of individual variation with the historical process of evolution. Dubinin concludded, "In dogmatically asserting its position, Lamarckism hinders the objective advancement of science by denying its most up-to-date facts."[10]

The articles by Serebrovskii and Dubinin left a strong impression. It was undoubtedly partly under their influence that in 1930 Solomon G. Levit rejected Lamarckian views in his speech on "Fundamental Tasks for the Society of Materialist Physicians."[11] Levit took note of the significance for medicine of the gains in the field of genetics. In his opinion, genetics ought to be taught in considerable depth to all future doctors in their general biology courses. As for the ideological battle, Levit claimed that "the fundamental danger is the mechanistic danger . . . Mechanism very clearly appears in all problems—in the problem of reduction, in the study

[9] Eugenii Sergeevich Smirnov, "Problemy ucheniia o nasledstvennosti" ["Problems of the Study of Inheritance"], *Estestvozn. i marksizm* [*Natural Science and Marxism*], 1929, *no. 2: 73-82.*

[10] Nikolai Petrovich Dubinin, "Genetiki i niolamarkizm" ["Genetics and Neo Lamarckism"], *Estestvozn. i marksizm* [*Natural Science and Marxism*], 1929, *no. 4:* 89.

[11] *Arkhiv AN SSSR* [*Archives of the Academy of Sciences of the USSR*], folio 421, opus 1, no. 1, p. 3.

of reflexes, especially sharply in the problem of Lamarckism versus Darwinism, in elemental Lamarckism, espoused by the majority of doctors, and in the problem of inheritance of favorable acquired traits."[12] Then he posed the question: Is mechanistic Lamarckism a proper materialistic teaching? He answered it himself: "No, it is not; but it quite logically fuses with idealism. . . . This fusion takes place in [the solution to] the problem of adaptation."[13] In the concluding remarks that summed up the lively debate occasioned by his speech, Levit spoke out most decisively against the inheritance of acquired traits.

The battle with mechanistic Lamarckism unfolded not only in the fields of biology and medicine, but also in the area of agricultural science and practice. Here the critics of Lamarckian views were confronted by an especially energetic opposition. The reasons for this were clarified in 1932 in an article by Serebrovskii.[14] Briefly describing the evolutionary views of Lamarck and Darwin, Serebrovskii noted that Darwin himself assigned a certain importance to Lamarckian factors of evolution, that is, to the direct influence of the environment and, to a lesser degree, to the exercise of organs. Following Darwin, and referring to his authority, "many biologists and even more animal breeders who called themselves Darwinians turned out to be eclectics even to a greater degree than Darwin. . . . All who continue to defend the 'purity' of Darwin's version of evolutionary teaching are actually much more clearly Lamarckians than was Darwin himself, who increasingly emphasized the role [of Lamarckian principles] toward the end of his life while confronting facts which today have completely lost their persuasiveness."[15]

Lamarck's views had as their premise long-standing, commonplace experience that had been, in Serebrovskii's expression, "'stood on its head' when an effect, for example the ability of muscles to enlarge through exercise, was taken for a cause, and a cause, the evolution of adaptations, was taken for an effect."[16] Evolutionary teaching was understood in just this spirit by animal breeders and was thus propagated in the Russian agricultural literature of the 1870s and later. This occurred particularly in the journal *Agriculture and Forestry*[17] and in textbooks, for example,

[12] *Ibid.*, p. 29.

[13] *Ibid.*, p. 30.

[14] Reference to this excellent article by Serebrovskii, which briefly and vividly characterized Lamarckian prejudices that were widespread among animal and plant breeders, makes it unnecessary to cite and evaluate appropriate examples from agricultural literature.

[15] Alexandr Sergeevich Serebrovskii, "Lamarkizm v zhivotnovodstve" ["*Lamarckism in Animal Breeding*"], *Problemy zhivotnovodstva* [*Problems of Animal Breeding*], 1932, *no. 8:* 9-10.

[16] *Ibid.*, p. 10.

[17] Articles under the by-line "Sochineniia Darvina v ikh otnoshenii k sel'skomu khoziaistvu" ["The Works of Darwin in Their Relation to Agriculture"] (*Sel'skoe khoziaistvo i*

(*contd.*)

General Animal Husbandry by P.N. Chirvinskii (1903). Serebrovskii cited a passage from this book where Chirvinskii stated that milking increases milk production of cows and sheep. Thus, for instance, Lazarian sheep, from whose milk Roquefort cheese is produced, have more than doubled their milk production in a period of one hundred years. Serebrovskii commented, "Certainly stimulation of the udder can facilitate milking of an individual animal, but one must not confuse this influence with inheritance of stimulation." By such confusion "evolution directly reduces to the physiological process of exercise which accumulates its effect from generation to generation, leaving the role of selection in its shadow." [18] Serebrovskii also mentioned the opinion of Redfield, who believed that "the longer horses were trained, the faster were the records attained by those horses' progeny." [19] Further on Serebrovskii wrote that few branches of animal husbandry supported the importance of exercise in breeding. Nevertheless, the second Lamarckian principle, that is, the direct influence of the environment on the origin of new hereditary traits, enjoyed a very wide acceptance in animal husbandry. Animal breeders gave special significance to the role of nutrition and conditions of maintenance. In Serebrovskii's words, proponents either ignored the role of selection or they forgot the fact that in the breeding of animals "not nearly every selection leads to an evolutionary advancement in the succeeding generation, but only those selections which entail hereditary traits.... If that question is not crucial for the breeders themselves, it is a decisive matter for the breed. Even a small favorable hereditary change is often infinitely more valuable in the fate of the breed than the greatest non-hereditary one.... Paraphrasing the humorous aphorism of Kuz'ma Prutkov, we may say, 'when looking at a fine bull, don't believe your eyes.'"[20] Nutrition and other conditions of maintenance and rearing indeed have great significance in that they allow the hereditary potential of the organism to express itself fully.

lesovodstvo [*Agriculture and Forestry*], 1872, *109*, were described in a book by Eduard Nikolaevich Mirzoian, *Istoriia izucheniia individual'nogo razvitiia sel'skokhoziaistvennykh zhivotnykh v Rossii* [*History of the Study of Individual Development of Agricultural Animals in Russia*] (Moscow: 1961).

[18] Serebrovskii (n. 15), p. 13. Wallace wrote about this earlier (see chapter 7).

[19] Serebrovskii, (n. 15), p. 13. Casper L. Redfield's views were creditably evaluated long before Serebrovskii by the geneticist Pearl, who pointed out Redfield's ignorance clothed in bombastic rhetoric concerning biological questions (Raymond Pearl, "Dynamic Evolution: Redfield's Theory of Inheritance of Training and Use Not Supported by Adequate Biological Evidence," *J. Hered.*, 1915, *6:* 245-256.) [Pearl was here responding to Redfield's *Dynamic Evoltion: A Study of the Causes of Evolution and Degeneracy* (New York and London: G.P. Putnam's Sons, 1914).]

[20] *Ibid.*, p. 15. ["Kuz'ma Prutkov" is the invention of the three nineteenth century poets: A. Tolstoy and the brothers Zhemchuzhnikov. We are grateful to Raissa Berg for this information.]

Nikolai Invanovich Vavilov
(1887-1943)

Nikolai Ivanovich Vavilov also opposed the opinions of the practical agriculturalists who defended the traditional view that pedigree and strain improvement resulted from the inheritance of acquired characters. Vavilov wrote, "There is an immense difference between a stance which supports the indisputable importance of agrotechnics, nutrition, and the conditions of developments and one which confuses heritable and nonheritable variation and thus returns to the ideas of Lamarck. Environmental conditions are powerful factors in selection. The environment can also give rise to hereditary changes, but as we know from the whole world of experience, from precise experiments, and from the basic postulates of Darwinism, these changes proceed in various directions and only by selection can one direct evolution. The evolution of the organic world bears witness to this, and the whole practice of selection and the experience of exacting genetics speaks in favor of it." Vavilov mentioned Klebs' book, *Willkürlich Entwickelungsänderungen bei Pflanzen,* which was translated by K.A. Timiriazev. He noted that "this great twentieth century experimenter, who worked especially in the field of experimental morphology, also reacted negatively to the possibility of hereditary transmission of acquired traits."[21]

[21] Nikolai Ivanovich Vavilov, "Kriticheskii obzor sovremennogo sostoianiia geneticheskoi

(*contd.*)

The founder of evolutionary morphology, Alexei Nikolaevich Severtsov, had a highly instructive view of Lamarckism, particularly concerning the question of the inheritance of acquired characters. From the very start of his career as evolutionist and theoretician Severtsov chose between the Lamarckian and Darwinian explanations of evolution. As early as 1912 he wrote in a monograph, "I believe that the indirect environmental influences on the living organism (Darwinian factors of evolution) play a much greater role in phylogenetic evolution than the direct environmental influences and exercise and non-exercise of organs (factors of Buffon and Lamarck)."[22,23] This thought was repeated almost word for word in his *Morphological Principles of Evolution* of 1939 (first published in German in 1931). In this book Severtsov simply added the name of Geoffroy Saint-Hilaire to those of Buffon and Lamarck.

To get a clear idea of how Severtsov regarded neo-Lamarckism, one should first examine his attitude toward the theory of Darwin. "As is well known, the essence of the explanation [of evolution by Darwin]," wrote Severtsov, "consists in the following: in all present-day animals and plants there are individual hereditary variations which biologically are either useful, indifferent, or harmful to their possessor."[24] Since Severtsov raised no objection to Darwin's teaching of random variations, he must have believed it to be completely sound. "Under a change in the conditions of existence," he continued, "that is, when the struggle for survival intensifies, animals possessing useful variations survive in the changed conditions. Through an accumulation of these useful variations the bodily organization of the progeny changes in the direction of greater adaptation to the new condition. . . . This is the essence of the simple and brilliant idea of the theory of survival of the best adapted during the struggle for existence—Darwin's theory of natural selection."[25] Severtsov noted that along

teorii selektsii rastenii i zhivotnykh" ["Critical Review of the Contemporary State of the Genetic Theory of Selection in Plants and Animals"], *Izbr. trudy v piati tomakh* [*Selected Works in Five Volumes*], 1965, *5:* 426–427. [Georg Albrecht Klebs, *Willkurlich Entwickelungsänderungen bei Pflanzen. Ein Beitrag zur Physiologie der Entwickelung* (Jena: Gustav Fischer, 1903); the last chapter of this work is on variation and mutation with a critique of Lamarckain Theory. The most accessible English work by Klebs on the subject is "The Influence of Environment on the Form of Plants," in *Darwin and Modern Science,* ed. Albert C. Seward (Cambridge: Cambridge University Press, 1909), pp. 223–246.]

[22,23] Alexei Nikolaevich Severstov, "Etiudy po teorii evoliutsii" ["Études on the Theory of Evolution"] and "Individual'noe razvitie i evoliutsii" ["Individual Development and Evolution"] (Kiev: 1912), cited according to Severtsov, *Sobr. soch.* [*Collected Works*], 1945, *3:* 85–86.

[24] Alexei Nikolaevich Severtsov, *Morfologicheskie zakonomernosti evoliutsii* [*Morphological Natural Laws of Evolution*], (1939), p. 71. [There is no English translation of this important work but see *Morphologische gesetzmässigkeiten der Evolution* (Jena: Gustav Fischer, 1931). All translated passages follow Blacher's text.]

[25] *Ibid.*, p. 72.

side the activity of this basic factor of natural selection Darwin "allowed that in certain situations the results of the altered conditions of existence (the factors of Lamarck and Geoffroy Saint-Hilaire) could become hereditary and influence the evolutionary course of animals."[26] Severtsov spoke of the difference of opinion over the importance of direct adaptation. He saw Haeckel, Spencer, and several American zoologists, especially paleontologists, as proponents of this mechanism. He saw in the front line of opponents August Weismann and Alfred Russel Wallace, who denied the inheritance of acquired traits and who regarded "natural selection of favorable hereditary variations as not only the chief, but the sole factor of evolution. . . . Many zoologists in England and on the continent supported Weismann's position."[27]

Next Severtsov considered the initial experiments of early geneticists, certain of whom, such as William Bateson and Wilhelm Johannsen, initially expressed doubt in the fact of evolution itself. Subsequently, "the huge successes which they achieved led them to consider the evolutionary problem. . . . Johannsen's study of pure strains at first led geneticists to believe that hereditary factors do not change over time—the hypothesis of the constancy of species. However, the study of suddenly arising mutations and the discovery of the dependence of mutation on changes in the external conditions led to the possibility of once more considering evolutionary questions."[28] Summarizing the results obtained by geneticists, Severtsov concluded, "We have every reason to believe that the extensive and valuable material already obtained by geneticists and the results of future research concerning mutations will be useful to proponents of natural selection."[29] There is no doubt that Severtsov saw future evolutionary theory in precisely this combination of the theory of natural selection and the study of mutations, not in the efforts of the neo-Lamarckians, who tried to explain evolution as direct adaptation to the surrounding environment.

Severtsov dedicated one chapter of the first Russian edition of *Morphological Principles of Evolution* to "a causal explanation of evolution" and to "the unsoundness of Lamarckism." "The theory of natural selection as a principle which explains the development of adaptive changes in animals and plants, has been analyzed in an immense quantity of examples by Darwin himself and by Wallace and a whole host of outstanding Darwinians."[30] Comparing the Darwinian and Lamarckian ideas of the motive

[26] *Ibid.*, p. 74.
[27] *Ibid.*, p. 74.
[28] *Ibid.*, p. 75.
[29] *Ibid.*, p. 76.
[30] *Ibid.*, p. 80.

Alexei Nikolaevich Severtsov
(1886-1936)

force of evolution, Severtsov first of all noted that "only through experimental research can one . . ." prove or disprove Lamarckism. Besides this, a theoretical analysis of the Lamarckian conception is necessary to clarify "just what this theory can contribute . . . to an explanation of the process of phylogenesis."[31]

Among the views of neo-Lamarckians Severtsov distinguished two positions: the first consisted of the principle of progressive evolution via intensified use of organs and the principle of regressive evolution via non-use of organs; the second consisted of the principle of adaptive response. For a discussion of the possible influence of exercise or non-exercise of organs, Severtsov turned to the example of knee calluses on the warthog (*Phacochoerus*). The Lamarckians, he asserted, reasoned that these calluses were the result of friction against the ground which became hereditary (warthogs crawl on their knees when procuring food). On the other hand, he argued, they could be explained very well by the proposal that "such habits could develop only in animals in whom the skin on the knees had been thickened by nature and in whom calluses rather than abrasions or wounds would form on the knees." Severtsov added that "the

[31] *Ibid.*, p. 82.

weakest point of neo-Lamarckism is the question of the inheritance of the results of exercise and non-exercise of organs. This question, which in Lamarck's time seemed so simple that it wasn't even thought worth discussing, now . . . has become extremely complex. A multitude of experimental studies by many geneticists speak against the inheritance of the results of exercise or non-exercise of organs."[32]

Arguing the groundlessness of the principle of progressive evolution via exercise, Severtsov pointed out that, for example, hypertrophy and the strengthening of exercised muscles is due to a thickening of the muscle fibers, not to an increase in their quantity. Thus, an increase in the volume of muscle tissue in ontogeny does not explain how there developed in phylogeny an increase in the number of fibers in separate muscle bundles, much less an increase in the number of bundles or of segmentally arranged muscles. Severtsov believed that analogous considerations should apply to the hypertrophy of glands caused by intensified function and to other similar situations.

Severtsov found it was still more difficult to apply the principle of progressive evolution by means of exercise to the nervous system and sense organs since in adult organisms the sensory cells do not multiply. The principle of exercise is clearly inapplicable to the development of passive (defensive) structures (scales of animals, thorns of plants) and even to the organs of attack (canine teeth, tusks, the saw of the sawfish, etc.), which are exercised so rarely that this "gymnastics," as Severtsov expressed it, could not be the cause of their hypertrophy. He wrote, in conclusion, that exercise led only to quantitative ontogenic changes, and therefore, qualitative phylogenetic "changes in the structure of organs cannot be explained on the basis of this principle."[33]

In Severtsov's opinion the use of organs likewise could not account for instances of the phylogenetic substitution of organs and functions, for example, the replacement of the notochord by boney vertebrae, of the cartilaginous skull by endochondral bones, or of Meckel's cartilage by protective bones. Likewise, the principle of regressive evolution by means of disuse was invalid. Severtsov considered this question in a work devoted to the phylogenesis of reducing organs. He discussed, in particular, the correlations in the reduction of segmented muscles, ribs, thoracic vertebrae, and the sacrum in the process of the reduction of limbs in serpentine lizards. "It seems completely unlikely that all of these correlations depended on the external conditions or on the use or disuse of organs (the Lamarckian principle) since . . . these variations exist in the embryos." In a footnote to this passage he noted that "it is very difficult to imagine what

[32] *Ibid.*, p. 85.
[33] *Ibid.*, p. 91.

kind of exercise needed to be done to transform a caudal vertebrum into a sacral one, or to move the developing rudiment of the pelvis from segment 58 to segment 59. Therefore, we reject explanations expressed in the Lamarckian spirit for the cases we have studied."[34]

In skates, which evolved from sharks possessing placoid scales over the entire body, these scales atrophied on the ventral side, that is, on the part of the body experiencing mechanical irritation from friction on the bottom. In flounders, *Pleuronectes flesus,* the scales are underdeveloped on the left side of the body, that facing the bottom. The same thing applies to the reduction of teeth in ancestors of present-day turtles and birds. Even if we believe that at one time the character of their food changed, it is nevertheless certain that the animals continued to eat and therefore to move their jaws. Functional stimulation of the teeth undergoing reduction did not, however, hinder their atrophy. "These facts," wrote Severtsov, "speak in opposition to the hypothesis of disuse as the cause of the reduction of organs."[35] Uninterrupted functioning often could not hinder reduction, in ontogenesis or in phylogenesis, of this or that part, for example, certain blood vessels. In these cases, as Severtsov noted, "we have no right to think that the cause of reduction was disuse of the atrophying organ. . . . Even were we to admit so controversial a principle as the inheritance of the results of use and disuse of organs, we coud use this neo-Lamarckian principle to explain only a comparatively small number of the adaptive changes known to us; the great majority of such changes do not yield to explanation by this principle."[36]

Severtsov also criticized the principle of adaptive response, according to which "an organism, finding itself in changed conditions of existence, reacts by adaptively changing its structure," and so transforming its organs in such a way that "these organs become suited to the new conditions of the environment."[37] "It would be very interesting, for example," Severtsov ironically continued, "for neo-Lamarckians to indicate just what changes in the environment evoked by way of a direct response the development of thorns and needles which protect plants from being trampled or eaten by herbivorous animals," or the development of burrs and wings on seeds, the pulp of fruit, and other adaptations.[38]

Results of experiments in which the structure of the alimentary canal changed under the influence of unusual food were, according to Severtsov,

[34] Alexei Nikolaevich Severtsow, "Studien uber Reduktion der Organe der Wirbeltiere," *Zool. Jahrb.*, 1931, *53*. (Severtsov, "Etiudy po reduktsii organov pozvonochnykh zhivotnykh," *Sobr. soch.* [*Collected Works*], 1945, *3:* 464.)

[35] Severtsov (n. 24), p. 93.

[36] *Ibid.*, p. 94.

[37] *Ibid.*, p. 94.

[38] *Ibid.*, pp. 94–95.

contradictory and therefore not credible. As to the question of the inheritance of changes which truly have arisen under the influence of changed environmental conditions, Severtsov considered this less problematic, since "neo-Lamarckians have yet to convince their opponents that the inheritance of so-called favorable acquired traits is the rule and not the exception."[39]

As Severtsov saw it, the discussion of the central thesis of neo-Lamarckism, namely the assertion that changes evoked by new conditions in the environment have an adaptive character, was critical. The mere fact that adaptive changes do occur was, in his opinion, a far cry from validating the neo-Lamarckian assertion, since newly arising traits are often indifferent or even harmful. In other words, it was highly unlikely that those evolutionary changes that were not subject to an explanation based on the exercise or non-exercise of organs arose as the result primarily of adaptive responses to the conditions of existence.

Severtsov did not rule out the possibility that certain adaptations to changes of climate arose in response to those changes. But he made it clear that such a response related to general, simple adaptations of a quantitative character and that in more complex instances "such an explanation is difficult to apply if we don't endow it with some mystical significance."[40] To illustrate this reservation Severtsov gave the example of the third eyelid of birds, which protects the eye from excessive light. It should have been the retina which changed in reaction to light stimulation and not the epithelial connective and muscle tissue surrounding the eye. The situation is the same in the development of eyelids and eyelashes in mammals. It is the cornea which experiences mechanical irritation, and it is quite unclear why in this case the tissues surrounding the eye should react with changes which provide protection for the cornea.

Severtsov considered it especially important to clarify the origin of those phylogenetic changes which concern interactions between various types of organisms, that is, changes that demonstrate adaptation in the biotic environment. He particularly made use of Serebrovskii's examples. Concerning the armor of paleoniscoidei and boney ganoids, which protected them from the bite of predators, Severtsov wrote, "From the Lamarckian viewpoint we apparently are to assume that injury to the skin inflicted by predators served as the stimulation to which ancestors of paleoniscoidei reacted with the development of complexly formed scales. Before accepting such an interpretation, it would seem desirable to find examples of a fish that as the result of wounds develops boney substance over its whole body (and not only in the area of injury). Of course, neo-

[39] *Ibid.*, p. 98.

[40] *Ibid.*, p. 99.

Lamarckians cannot supply such proof."[41] Severtsov posed the same questions for Lamarckians concerning the development of poison fangs and their auxiliary adaptations in snakes and concerning the development of needles in cacti. He continued, "We hardly have the right to suppose that . . . adaptive responses of organisms to changes in the biological environment actually occur. This [process] is the more unlikely because often changes in the biological environment do not and cannot influence the animal directly. For instance, a new enemy influences its prey only when it kills it, that is, when it is already too late for the prey to change."[42] The persuasiveness of Severtsov's objections to neo-Lamarckism and of his deliberations in favor of a Darwinian explanation of evolution is quite obvious.

Severtsov felt that the question of the inheritance of acquired traits had not been answered in sufficient detail. He himself argued one aspect of the problem with great insight. In his opinion, the examples of the inheritance of acquired changes which had not been verified by more careful research, such as experimental melanism in butterflies in studies by Max Standfuss and Emil Fischer, provided no basis for extrapolation. In particular they did not warrant the assumption of the inheritance of the results of exercise and non-exercise of organs. In light of the data of Standfuss and Fischer, Severtsov asked, does it become likely "that degeneration of digits II and IV in the ancestors of the horse, which occurred because one of the ancestors supported itself more weakly on them, became hereditary? . . . How was this essentially negligible change in the size of the metacarpals, metatarsals, and phalanges reflected in the egg and sperm cells of the progeny of the horse? In what manner did the minor quantitative changes in the bones of digits II and IV change the structure of the sex cells so that, after a very great number of cell divisions, these changes were reflected in the metacarpals, metatarsals, and phalanges of the same digits in the progeny of these horses in the same direction, that is, in the direction of diminution?"[43] Is it not surprising that an evolutionary morphologist, whose scientific activity in content and methods was so far from the problems and methods of cytologists and geneticists, could formulate with such clarity the basic question which needed answering for an informed discussion of the inheritance of acquired traits? Severtsov well understood that it was imperative to work out the whole chain of events, beginning with changes in organs remote from the reproductive elements, and leading, as Lamarckians asserted, to the corresponding changes in hereditary information in the sex cells. Changes in genes must therefore be stable so

[41] *Ibid.*, p. 100.
[42] *Ibid.*, p. 201.
[43] Severtsov (n. 24), p. 102.

that they are preserved through many mitotic and meiotic divisions. They must be preserved in such a way as to assure the reproduction in progeny of exactly the same traits as were acquired by their predecessors. Severtsov quite justifiably doubted that such a chain of events would be discovered.

Severtsov, like Serebrovskii, convincingly showed that phenomena of adaptation find a non-contradictory materialistic explanation in the Darwinian principle of natural selection. The task of constructing an evolutionary theory founded on a consistently materialistic conception of living phenomena demands a logically and empirically rigorous resolution of the question of inheritance of acquired characters.

Arguments against Lamarckism and in support of evolution through natural selection were supplied by Wallace, Weismann, Detto, and Timiriazev, as well as by Darwin himself. Timiriazev thought that, of his contemporaries, Detto was the one who most successfully showed the unsoundness of the principle of direct adaptation.[44]

Carl Detto made a detailed critique of the theory of direct adaptation. With complete justification he asserted that the theory that external influences evoked precisely those changes necessary to assure the survival of the organism was inconceivable without assuming a willful act underlying such processes and directing them. After all, only in the conscious realization of a desire is the cause determined by a goal. Theories which admitted the possibility of direct adaptation assumed that *ekologizmy,* or states of adaptiveness, arose from an ability of organisms to change themselves expediently in accordance with changes in the environment. In short, structure and behaviour adapted themselves to the environment. Proponents of such theories took for granted just that which should be explained and was indeed explained by the theory of natural selection.

An example of a change in an organ that represents a functional adaptation is the modification of bones under the influence of function. Boney substance is laid down in the places of great stress. This sort of phenomenon does not explain, however, the development of functional changes in phylogenesis. It is for just this reason that Lamarckism is not capable of explaining the origin of adaptive traits. The explanation was supplied by Darwin. Its essence was to be found in the origin of traits that arose independently of the character of the external influences and that could assure survival, that is, prove adaptive under the given conditions. "Chance," Detto maintained, "decides the question—to be or not to be. This chance is

[44] Kliment Arkadievich Timiriazev, "Istoricheskii metod v biologii" ["The Historical Method in Biology"], *Soch.* [*Works*], 1939, *6:* 162. Timiriazev had in mind Carl Detto's book, *Die Theorie der direkten Anpassung und ihre Bedeutung für das Anpassungs- und Deszendenzproblem, Versuch einer methodologischen Kritik des Erklärungsprinzipes und der Botanischen Tatsachen des Lamarckismus* (Jena: Gustav Fischer, 1904).

the logical postulate which scientifically explains the origin of organic adaptation. The philosophical power of the theory of selection, that is, the power of Darwinian thought, lies precisely in this chance.''[45]

In *Dialectics of Nature* Friedrick Engels commented on the profundity and novelty of Darwin's generalization. ''Darwin in his epoch-making work set out from the widest existing basis of chance.''[46]

Basing itself on a metaphysical conception of chance, absolutized and understood as the antithesis of necessity, anti-Darwinism, in its diverse forms, objected precisely at the point of admitting the role of chance in the process of speciation. Among the vitalists who spoke in this vein was Hans Driesch, who called Darwinism ''a recipe for how to construct a house of a definite style by the mere random piling up of rocks.''[47] Lev Simonovich Berg took the same viewpoint when he attempted to contrast Darwin's teaching, which Berg called ''tikhogenesis'' [from Greek τύχη —chance], with his own conception of the evolutionary process—''nomogenesis'' [νομοδ —law]. ''The origin of some forms from others is subject to natural law and proceeds in a definite direction. It is not dependent on the caprice of chance.... What sort of cause forces an organism to change in a definite direction is as yet unknown to us.... An organism has the capacity to adapt itself actively to the environment, revealing thus the apparent presence of some kind of internal regulating principle.''[48] In contrast to the Darwinian understanding of the source of adaptive, that is, expedient, traits by the natural selection of useful variations, Berg believed that ''adaptation is a fundamental property of a living being.... One of the consequences of the principle we espouse of primary adaptation is the doctrine of the influence of exercise and non-exercise of organs, or Lamarckism.''[49]

Georgii Vasilievich Nikol'skii many times assumed a Lamarckian position in opposition to the basic tenets of Darwinism.[50] He advocated the idea

[45]Detto (*ibid.*, p. 190.)

[46]Karl Marx and Freidrich Engels, *Soch.* [*Works*], vol. 20, p. 535. [Quotation taken from Friedrich Engels, *Dialectics of Nature,* trans. Clemens Ditt (New York: International Publishers, 1940), p. 234.]

[47]Hans A.E. Driesch, *Vitalizm, ego istoriia i sistema* [*Vitalism, Its History and System*], (Moscow, 1915), p. 145. [Driesch, *The History and Theory of Vitalism,* trans. C.K. Ogden (London: Macmillan and Co., 1914). This passage cannot be identified in the English version. The closest consists of: ''Then Darwinism, which explained how by throwing stones one could build houses of a typical style . . . ,'' p. 137.]

[48]Lev Simonovich Berg, *Nomogenez ili evoliutsiia na osnove zakonomernostei* [*Nomogenesis, or Evolution Based on Natural Laws*] (Petrograd, 1922), pp. 47-48. [Berg, *Nomogenesis, or Evolution Determined by Law,* intro. D'Arcy Wentworth Thomson; trans. J.N. Rostovtsow (London: Constable & Co., 1926) quotations are translated from Blacher's text.]

[49]*Ibid.*, p. 6.

[50]Georii Vasilievich Nikol'skii, ''O nekotorykh voprosakh problemy vida'' [''On Certain Questions of the Problem of Species''], *Zool. zhurn.* [*Zoological Journal*], 1953, *32:* 820-827; ''O nekotorykh obshchikh problemakh biologii'' [''On Certain General Problems of Biology''], *Biull. Mosk. ov-va ispytat. prirody* [*Bulletin of the Moscow Society of Researchers in Nature*], 1953, *58:* 48-56; ''Ob izmenchivosti organizmov'' [''On Variability of Organisms''), *Zool. zhurn.* [*Zoological Journal*], 1955, *34:* 723-733.

of direct adaptation in preference to the Darwinian principle of random variation and, in fact, did not acknowledge natural selection as a fundamental factor in speciation. Natural selection, in Nikol'skii's opinion, ''is neither a creative nor a specific biological factor.''[51]

An article by K.G. Konstantinov presented factually substantiated arguments against Nikol'skii's anti-Darwinist views.[52] By resorting to several examples, Konstantinov refuted Nikol'skii's assertion of the self-adaptive character of the process of variation. The adaptive features of an egg shell (its hardness, structure, coloration) could not have arisen as the result of direct adaptation to both the conditions of the surrounding environment and the conditions inside the bird where the egg developed. The red color of many marine invertebrates (sea stars, ophiurans, crabs, shrimps, actinians) and fish (sea perch) occurs in depths where no red rays penetrate. The appearance of mimicking forms occurs in the absence of any contact between model and imitator. Direct adaptation cannot explain the appearance and fixation of instincts in worker bees since they do not produce offspring.

Among the anti-Darwinists of comparatively recent times, one may count the anatomist Hans Böker, whose views were set forth in an article, ''Transformation of species by reconstruction; reconstruction through active reaction of organisms.'' Böker defended the view that for evolution it is not the change in individual traits that is significant, but ''the reconstruction of an anatomical construction, which altogether renders the animal adapted.''[53] Such reconstruction, in Böker's opinion, was the result of an active response, without which ''there is no adaptation but only subjection to chance, chaos, annihilation.... As soon as the ecological-ethological equilibrium is destroyed, there arises an anatomical reaction in the form of a reconstruction.... While passive mutations are random and are neither future oriented nor purposeful, the reconstruction always deals by means of an active response with a creation of Sinnegefügen.''[54]

''The actual transformation of organisms,'' Böker further wrote, ''is always an active, creative act by the organisms themselves, which corres-

[51]Nikol'skii, ''On Variability of Organisms'' (*ibid.*, p. 730).

[52]K.G. Konstantinov, ''Napravlennaia izmenchivost' ili estestvennyi otbor?'' [''Directed Variability or Natural Selection?''] *Zool. zhurn.* [*Zoological Journal*], 1956, *35:* 972-977.

[53]Hans Böker, ''Artumwandlung durch Umkonstruktionen, Umkonstruktion durch aktives Reagieren der Organismen,'' *Acta biotheor.*, 1935, *1:* 17-34. [Quotation follows the German on p. 19.]

[54]*Ibid.*, pp. 25-26.

ponds to their internal world. In confusing active adjustment (Einpassung) with passive adaptation (Anpassung), Darwinism as well as Lamarckism is in the final analysis found wanting. Both assign to the external world the active role in the transformation of species." In accordance with this view, Böker limited inheritance of acquired traits to those properties which arose as the result of active "adjustment," and he denied the inheritance of traits which were passively evoked by conditions of the surrounding world. "I do not doubt that the inheritance of actively formed structures, i.e. of those whose emergence the organism desired, will some day be demonstrated."[55]

Very similar ideas were repeatedly expressed by Paul Wintrebert, who recently published, one right after another, two lengthy books with similar titles: *The Living Being—Creator of its own Evolution* and *The Development of a Living Creature Under its own Power.*[56] Wintrebert was sure that "a living being conquers the environment by reacting to its influences through creative functions inherent in that being's individualized macromolecular structures. These creative functions serve as evidence of chemical reason, simultaneously conscious and unconscious. This position . . . which continues the work of Lamarck, should bear the name of the originator of the concept; I call it chemical Lamarckism."[57] Wintrebert described the biochemical mechanism of hereditary adaptation which constituted the basis of his theory. When there emerged an adaptive trait, that is, a change in the structure and function of an organ, it acted as an antigen by producing an adaptive antibody; the latter, adjoining the nucleoprotein, gave rise to a new gene.[58] Further on Wintrebert elaborated this idea. According to his conception, while the demand for a new or changed function remained unsatisfied because of the absence or underdevelopment of the corresponding organ, a "toxin of functional insufficiency" was built up in the organism for the neutralization of an antigen, that is, a deoxyribonucleic antibody or hormone was formed and that hormone in combination with the species' nucleoproteins, became the source of a new or changed gene.[59] This "concretization" not only failed to make Wintrebert's hypothesis more convincing and credible but revealed more graphically its completely speculative nature.

[55] *Ibid.*, p. 28.

[56] Paul Wintrebert, *Le vivant créateur de son évolution* (Paris: Masson et cie., 1962), 416 p. Wintrebert, *Le Développement du vivant par lui-meme* (Paris: Masson et cie., 1963). Only the first of these books is further quoted since the second, published one year later, did not contain any new arguments in support of the author's views. [All translations follow Blacher's text.]

[57] Wintrebert, *Le vivant créateur de son évolution*, pp. 4–5.

[58] *Ibid.*, p. 13.

[59] *Ibid.*, pp. 84, 131, 304, 306, 331.

Wintrebert engaged in a polemic with Jean Rostand, who consistently spoke against Lamarckism, referring especially to the failure of experiments to show the inheritance of acquired traits. These failures, according to Wintrebert, could be explained by the fact that the experiments had used injuries to the organism for acquired traits rather than adaptations actively produced by the organism itself, and by the fact that the experiments were conducted in a laboratory environment. Wintrebert thought that analogous experiments could be conducted under natural conditions, that is, by allowing the organism to produce a preliminary adaptation, and then after its use, by clarifying the biochemical nature of the hormone secreted by the changed organ, and [finally] by cytologically establishing the appearance of a new gene. By such experimentation, Wintrebert hoped, not only would the inheritance of acquired traits be proven, but the chemical mechanism of its origin would be revealed. In speaking of experiments in nature, however, Wintrebert himself emphasized the necessity of caution in choosing the subjects for study and in establishing their genetic purity.[60, 61]

Wintrebert returned several times to his hypothesis of the adaptive deoxyriboneucleic hormone-antibody although he cited no proof of its veracity. He also stated more than once that "living material possesses reason," that an organism "not only derives energy from the surrounding environment, but regulates the environment, subduing it and using it selectively for its own aims."[62] Wintrebert reproached Darwin for his negative attitude toward Lamarck, namely toward the latter's opinion that adaptations depend on the will of animals.[63] According to Lamarck, as Wintrebert understood his views, "adaptation is the primary cause of evolution."[64]

Wintrebert strove to preserve not only the vitalistic thought of Lamarck that organisms change in answer to the conditions of their existence but he strove to preserve Lamarck's proposition, which had lost all significance, that these changes depend on the perception of requirements and on the will of the animals.

If Wintrebert's compositions had been published one hundred years ago, one could have dismissed them in one phrase, adding his name to the names of a long line of other authors who adhered to similar views at that time. But the appearance of Wintrebert's books in the sixties of the twentieth century compels one to speak of it in more detail and to give it due consideration from the perspective of contemporary science.

[60] *Ibid.*, pp. 31, 304.

[61] *Ibid.*, p. 94.

[62] *Ibid.*, pp. 116–117.

[63] *Ibid.*, p. 299.

[64] *Ibid.*, p. 381.

Lamarckian views are held by certain other contemporary authors besides Wintrebert, including Philip G. Fothergill in America and Franck Bourdier in France. Bourdier, referring only to data in the literature, resurrected the old argument of Lamarckians that the inheritance of acquired characters can be realized only when the agent of change acts for many centuries and therefore is not reproducible under laboratory conditions. He referred to geological and cosmological laws, the truth of which was supported not experimentally but by indirect reasoning.[65]

Jean Rostand wrote about the historical significance of Lamarckism and Darwinism and the question of the inheritance of acquired traits. According Lamarck's genius its rightful due and drawing upon experimental data which were reliable, Rostand acknowledged that "Lamarck's explanation of the mechanism of evolution did not stand up to the test of time.... Contrary to Lamarck's opinion, changes acquired by the individual are not transmitted to progeny."[66] Contrasting the views of Darwin, who believed that acquired traits could be inherited in certain cases, with the views of Weismann, who "decidedly rejected the inheritance of acquired traits," Rostand concluded, "Now it is established that acquired changes which depend on the surroundings (phenotypic) disappear along with the individual which displayed them: they are unavoidably transitory, cannot be transmitted to progeny, and play no role in evolution."[67]

An article by Armen Levonovich Takhtadzhan gave an excellent analysis of the contrast between the theory of evolution based on direct adaptation and that based on natural selection. Takhtadzhan demonstrated that all known forms of the evolutionary process are subject to statistical laws. He came to the conclusion that "a rejection of this statistical principle logically leads either to various theories of autogenesis, orthogenesis, aristogenesis, nomogenesis, and the like, or to one of the varieties of neo-Lamarckism, from psycho-Lamarckism to mechano-Lamarckism and 'Creative Darwinism.' The most characteristic trait of neo-Lamarckism... is the belief in so-called 'direct adaptation,' based on the effective transmission of 'acquired traits.'"[68]

The basic dogma of the hypothesis of direct adaptation, Takhtadzhan continued, "is the belief in the ability of each individual to make an adaptive, heritable response to the influence of the surrounding environment.... Variation directly created adaptation without the creative work of selection."[69] Here Takhtadzhan used a comparison which Serebrovskii

[65] Franck Bourdier, "Le lamarckisme et la raison," *Cahiers rationalistes*, 1967, *no. 252*.

[66] Jean Rostand, Esquisse d'une histoire de la biologie (Paris: Gallimard, 1945, p. 106. [Quotation taken from the French.]

[67] *Ibid.*, p. 184.

[68] Armen Levonovich Takhtadzhan, "Priamoe prisposoblenie ili estestvennyi otbor? (O statisticheskikh zakonomernostiakh biologii)" ["Direct Adaptation or Natural Selection? (On the Statistical Natural Laws of Biology)"], *Bot. zhurn.* [*Botanical Journal*], 1957, *42:* 603.

[69] *Ibid.*, p. 604.

had once proposed: the idea that evolution is the result of direct adaptation is comparable to the idea that the armor of tanks and warships thickens under the influence of blows from enemy shells.

Takhtadzhan further examined those examples of adaptive plasticity of organisms upon which Lamarckians had offered in vain as evidence of the origin in ontogeny and fixation in phylogenesis of adaptive traits. Changes in the form of the leaves of amphibious plants, for example, water plantain or amphibious buckwheat, are not newly acquired traits, but the manifestation of an ability to react to external influences that was acquired through natural selection during the process of past evolution. Therefore, the individual adaptive plasticity of organisms is the result of evolution and not the cause of adaptive evolutionary changes. Takhtadzhan specially considered the question of the inheritance of acquired individual changes. He noted that if one assumes the formative influence of somatic cells on sex cells, then likewise one should assume the influence of some somatic cells on others. In this case "changes in each part of the organism should be transmitted to all other parts, first of all, of course, to the neighboring parts.... Thanks to the mutual hereditary influences of all parts, the organism should in time dedifferentiate, that is, all of its parts should gradually begin to resemble one another, and... the organism sooner or later should become a formless mass." Not one Lamarckian would agree with such a deduction, Takhtadzhan thought, but something similar—"the hereditary interaction of somatic parts"—is assumed by Lamarckians for cases of so-called "vegetative hybridization. Therefore, the escape for Lamarckism is a tacitly acknowledged assumption that acquired changes are transmitted by some isolated path to the sex cells only. What the nature of this mysterious path is, Lamarckians do not explain."[70]

Ivan Ivanovich Schmalhausen examined the attempts to defend the idea that variations possess a direction which is appropriate for the changes in external conditions. He noted that such changes which might be wrought by influences are greatly limited by the organism's system of regulatory mechanisms. We might assume that external influences act on the synthesis of specific proteins which are related to the structural traits of the cell. For example, the structure of molecules of RNA might be altered. But when that influence is gone, unaltered RNA will once again be synthesized since its structure is determined by molecules of DNA. If the external influence acts also on the structure of DNA then "this is such a complexly mediated change that one cannot even think of a simple mechanism. This would objectively be the random change which we should call a mutation."[71]

[70] *Ibid.*, pp. 606–607.

[71] Ivan Ivanovich Schmalhausen, "O determinizme i statisticheskikh zakonakh v uchenii o nasledstvennosti" ["On Determinism and Statistical Laws in the Study of Heredity"], *Bot. zhurn.* [*Botanical Journal*], 1958, *no. 8* rpt. in Schmalhausen, *Kibernetichesk ie voprosy biologii* [*Cybernetic Questions of Biology*] (Novosibirsk: 1968), p. 184.

CHAPTER 11

The Classification of Changes Caused by External Influences

One of the most objective surveys of work concerning the problem of the inheritance of acquired traits is an extensive chapter in Emile Guyénot's book, *Variation and Evolution.*[1]

Rather than cover the entire history of the question, Guyénot began his discussion with Lamarck's views. He correctly noted that Lamarckian theory, mechanistic in intent, actually bears a finalistic, or teleological, character. According to Lamarck, living organisms responded to influences of the environment with adaptive changes. Without this "hidden finalism," as Guyénot expressed it, Lamarck's theory could not be called a theory of evolution, a theory of adaptive changes. It was precisely this "hidden finalism, disguised as determinism" which was the source of the success of Lamarck's theory among certain naturalists and philosophers who were dissatisfied with Darwin's materialistic theory.

One must agree with Guyénot that Lamarckians abused the argument that prolonged periods were necessary for evolutionary changes under the direct influence of external factors. Naturally, they evoked this argument only when discussing the negative results of experiments designed to prove the inheritance of acquired characters. In literally all of the experiments which they regarded as successful demonstrations the Lamarckians were for some reason not perplexed by a short duration of the altering influence (sometimes as short as a single generation).

The Lamarckians sharply criticized Weismann's concept of the essential difference between the reproductive elements of the organism, the germ-plasm, and all other parts of the organism, the soma, which excluded the specific influence of the soma on the germ-plasm. In Guyénot's opinion the difference between the germ-plasm and the soma was analogous to the difference between any two parts of the organism—between a limb and a tail, brain and liver, and so on. There was little basis for thinking that damage, atrophy, or hypertrophy of the eye could fundamentally influence, for example the structure of the hand. By the same

[1]Emil Guyénot, *La Variation et L'evolution,* vol. II, *L'evolution* (Paris: Gaston Doin, 1930), p. 414 [Translations taken from the original French].

Emil Guyénot
(1885-1963)

token it was doubtful that hypertrophy of the biceps, the appearance of anchylosis in the elbow joint, a change in the structure of the eye or a functional change in the brain (appearance of new habits) were reflected in a specific way in the germ-plasm. Moreover, in order for a change in bones, muscles, or any other body part which arose during an individual life to be passed on to its offspring, a correlative change in the germ-plasm was not of itself sufficient. It was absolutely essential that this change be specific, that is, that it produce in the progeny the same (or nearly the same) change which was induced in the parents by the environmental influence. An *a priori* assumption was made, based on the principle of functional correlations between organs, that the effect of different parts of the body on the germ-plasm could be realized through the nervous system or by means of specific substances like hormones circulating in the blood. Who would dare to assert, asked Buyénot, that the nerve fibers actually transmit influences which cause the appropriate changes in the germ-plasm, with the result that the progeny's development is altered in the same manner as the parents' had been? In his opinion it was inconceivable, for example, that a shortage of a thyroid hormone in a parent individual should stimulate changes in its germ-plasm which would result in a corresponding change in the level of that hormone in the offspring. The number of hormones with

definitely established formative functions was quite limited. But the hormone hypothesis of the hereditary transmission of acquired traits assumed the existence of separate hormones supposedly manufactured by the bones, muscles, joints, etc., and what is more, specific hormones manufactured by each individual muscle, bone, and joint. Guyénot considered the idea thoroughly improbable that an unlimited number of specific substances circulated in the blood, reached the germ-plasm, and caused there specific transformations.

The concept of inheritance of acquired characters, as Guyénot summed it up, was by no means as natural and logical as its proponents would have us believe. It demanded totally inconceivable physiological assumptions. We could overcome the inconceivability of these assumptions, which generally speaking do not themselves serve as evidence against such a hypothesis, only by finding indisputable evidence that such inheritance took place. Guyénot listed the requirements for rendering acceptable any experiments which purported to demonstrate the inheritance of acquired traits.

First of all, it is necessary to prove that a change actually does arise originally in the somatic parts of the organism (this change may be called a *somatsia*) and that it is only secondarily reflected in a change in the germ-plasm (a change called a mutation). In other words, those experiments in which the altering factor acts or is capable of acting directly on the germ-plasm are unsuitable as evidence of the inheritance of acquired characters. But equally unsuitable for this goal are those cases in which the influencing factor causes changes in the soma of the parents (*somatsia*) and simultaneously causes changes in the germ-plasm which yield a mutation in the offspring, whose external expression resembles the parents' *somatsia*.

Secondly, one needs precise information about the genetic make-up of the organisms used in the experiments. For this reason experiments on material taken directly from nature are unsuitable since it is unknown what hidden (recessive) hereditary factors are present in a given natural population.

With regard to plants and animals bred under laboratory conditions, preliminary examination over the course of several generations is required to see whether or not the organism carries hereditary factors in a recessive form. The existence of such factors could cause the appearance of a trait similar to that induced by the experimental influences utilized. Guyénot correctly noted that all of the experiments the results of which had been interpreted as evidence of the inheritance of acquired traits had failed to meet rigorously this requirement.

Thirdly, it is essential to demonstrate an unambiguous causal link between the change and the factor which actually gave rise to it. Nonetheless where many reports asserted that such a causal link was demonstrated, it turns out, in truth, that a describable change appeared in only an insignificantly small number of the hundreds of individuals subjected to an influence.

Fourthly and finally, it is essential to eliminate the possibility of so-called false inheritance, that is, the appearance of changes due to one or another chemical influence on the cytoplasm of the egg only, while the hereditary (nuclear) structures remain unchanged. Examples of false inheritance are seen in the experiments of Ludwick Sitovski (Sitowsky), in which he fed the larvae of the clothes moth, *Tineola biseliella*, wool saturated with a solution of Sudan-Red, which dyes fat red. In the process the fatty inclusions of both the somatic and sex cells were colored. Consequently the dye also appeared in the tissues of the offspring which developed from these eggs.[2]

The experiments of Frederick Wenzel Hofmann present an analogous case. This investigator studied the influence of chloral hydrate on the development of beans. The frequency (percentage) of the appearance of anomalies decreased in seven succeeding generations in the following manner: 73, 67, 47, 51, 8, 4, 0. The anomalies were transmitted only by the ova and not by pollen, making this a case of so-called false inheritance.

Summarizing the above requirements for rendering conclusive experiments designed to verify the inheritance of acquired traits, Guyénot said it was essential that investigators "use a pure line, verified with respect to its genotype; utilize factors incapable of acting directly on the germ-plasm; determine exactly the causal link between the action of the factor and the results obtained; verify finally that the new variations which emerge, having appeared in a sufficient number of the investigated individuals, are actually transmitted by the germ-plasm of the sex cells and are recovered in many successive generations after a return to normal conditions."[3]

Concerning the Lamarckian views which were widespread in the twenties, Guyénot noted that the discussion of problems was hindered by the fact that in support of their hypothesis the Lamarckians sometimes conducted experiments in which the germ-plasm was influenced directly—cases of induced mutations. In other experiments the offspring of parents that had been subjected to one or another influence indeed displayed changes, but changes which differed from those of the parents. These experiments, as Guyénot wrote, "have nothing in common with the ideas of the inheritance of acquired traits and create hopeless confusion. When reading some of these treatises you risk losing the main point of the matter, and you receive the impression that the inheritance of acquired traits has been proven, when in reality a totally different problem is discussed."[4]

[2] Ludwik Sitowsky, "On the Inheritance of Aniline Dye," *Science*, 1909, *30*: 308.

[3] Guyénot, (n. 1), pp. 33–34. [In the French text this entire passage is placed in italics.]

[4] *Ibid.*, p. 34.

Table 1

Parents	Offspring	Nature of results
I. Factors acting directly on the soma alone		
a) Local change (hypertrophy, atrophy, etc.)	No reflection	1) *Somatsia*
	Reflection of a different nature	2) Unlikely
	Specific reflection (same change as in parents)	3) Inheritance of acquired traits
b) General change (with or without local change)	No reflection	4) *Somatsia*
	Some reflection	5) Possible
	Specific reflection (same as in parents)	6) Inheritance of acquired traits
II. Factors acting directly on the germ-plasm or simultaneously on the soma and germ-plasm		
a) Local change	No reflection	7) Germ-plasm not affected
	Some reflection	8) May be an induced mutation
	Specific reflection	9) Accidental coincidence of results of direct action on the soma and germ-plasm (mutation)
b) General change (poisons, alcohol)	No reflection	10) *Somatsia*
	Some reflection	11) For example, hereditary alcoholism
	Specific reflection (for example, the same damage caused by alcoholism as in parents)	12) Unlikely event, possibly induced mutation
c) No change	Local or general change	13) Induced mutation

In order to end ambiguities, Guyénot compiled a table (table 1) which classified the variety of possibilities according to: the nature of the influencing external factors, the character of the changes (local or generalized) or the absence of any change, and the manner in which changes induced in the parents were reflected in the offspring (absence of changes in the latter, changes similar or dissimilar to those of the parents). Guyénot concluded that the concept of the inheritance of acquired characters, in the precise meaning of that expression, corresponded to cases number 3 and 6 of the thirteen possibilities given in the table. These were cases of corresponding alterations in the germ-plasm that took place under the influence of local or general somatic changes. It was precisely these cases that Guyénot held to be highly improbable.

Bernhard Dürken introduced a similar classification of alterations which might be caused by external influences in his *Foundations of Developmental Mechanics*. In his schematic diagrams he portrayed: 1) direct action on the germ-plasm (Dürken calls it "the basis of reaction"—Reaktionbasis, see figure 1, A), 2) parallel induction with a change of the entire soma (figure 1, B,a) or of a small part of it (figure 1, B,b), and 3) somatic induction with a change in a portion of the soma causing a change in the "basis of reaction" (figure 1, C) or change in the whole soma with the same consequence. (figure 1, D,a and b—two consecutive phases of the induction process). Dürken felt that the possibility of parallel induction was grossly exaggerated. As for a partially altered soma influencing the germ-plasm—inheritance of acquired traits in the Lamarckian sense—he felt "it is more than doubtful that such induction ever occurred; in any case grave objections may be raised against this possibility, and nothing resembling it has so far been experimentally obtained."[5] Dürken envisaged several other more complex paths of action of somatic changes on the germ-plasm. In contrast to Guyénot, who denied somatic induction, Dürken avoided a specific conclusion, though it would seem that this possibility follows directly from his diagram.

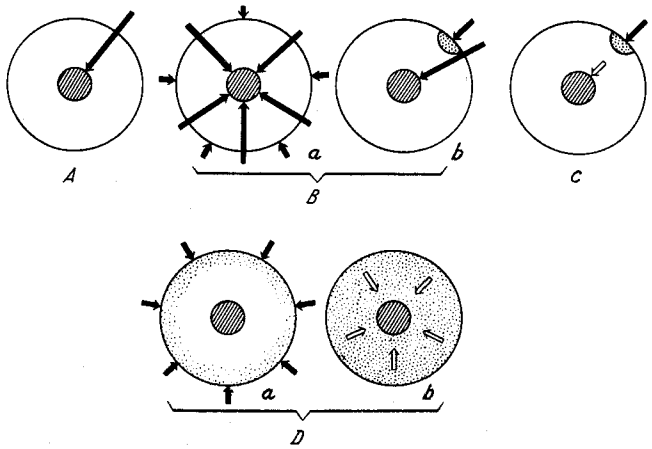

Figure 1. Diagram of possible influences of external factors (according to Bernhard Dürken, simplified). Outer circle—soma; inner circle—germ-plasm ("basis of reaction"); black arrows—external factors acting either on the soma or directly on the germ-plasm. For the meanings of letters, see the text.

Almost simultaneously with Dürken and Guyénot, Mikhael Mikhailovich Zavadovskii contrasted the various conceivable manners of change in the organism brought under the influence of external factors and

[5] Bernhard Dürken, *Grundriss der Entwiklungsmechanik* (Berlin: Gebrüder Borntraeger, 1929), S 135.

Mikhail Mikhailovich Zavadovskii
(1891-1957)

represented them in a diagram more illustrative than Dürken's (figure 2).[6] The external factor in this diagram is shown by the letter R; the solid arrow indicates its effect. The straight dotted arrows indicate the response of the somatic tissue or the germ-plasm to the altering influences. A parallel positioning of the dotted arrows indicates an identical change in traits in the parents and offspring, whereas diverging arrows indicate dissimilar changes in parents and offspring. A curved dotted arrow signifies an influence of the soma on the germ-plasm.

The diagram includes the following possibilities:

1) The external influence causes a change in the soma but does not reach the germ-plasm, which therefore remains unchanged (A_1).

2) The external influence changes the soma, the change of which has an effect on the germ-plasm. The changes in the germ-plasm are such that in the next generation a new trait appears, but it is not identical with the

[6] Mikhail Mikhailovich Zavodovskii, *Dinamika razvitiia organizma* [*Dynamics of the Development of the Organism*] (Moscow: 1931). The diagram is given in a somewhat simplified form, as it is reproduced in a book by Leonid Ia. Blacher, *Kurs obshchei biologii dlia meditsinskikh institutov* [*A Course in General Biology for Medical Schools*] (editions 1-4, 1935-1944.)

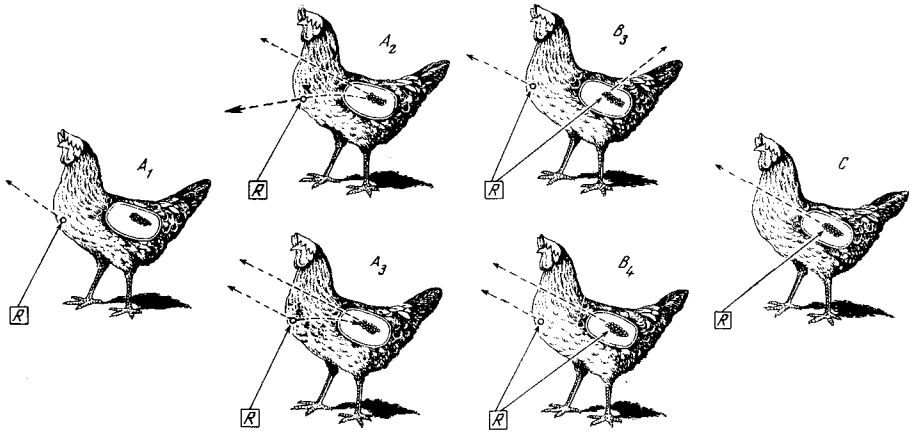

Figure 2. Diagram of various influences on the soma and sex cells (according to M.M. Zavadovskii, simplified). Explanation in text.

altered trait of the parents (A_2).

3) The external influence affects the soma and the germ-plasm simultaneously. The changes in the progeny could conceivably be dissimilar (B_3) or similar (B_4) to those in the parents. Detto has termed this last possibility parallel induction.

4) The external influence does not affect the soma and has an altering influence only on the sex cells (germ-plasm) (C).

Cases A_3 and B_4 satisfy the criteria for phenomena of the "inheritance of acquired characteristics"; they show somatic and parallel induction with a change in the sex cells corresponding to the change in the soma. Cases A_1 and C do not qualify as inheritance of acquired traits since in the first case there is no inheritance and in the latter there is no acquired trait. Cases A_2 and B_2 likewise do not qualify since in both cases one trait is acquired but another is inherited.

Cases A_1, A_2, B_2, and C are entirely possible. A multitude of facts testify to the possibility that external influences may cause somatic changes, that is, somatsia (A_1), and blastogenic changes, that is, induced mutations (C). It is possible, though it has not been shown directly, that the changes arising in the soma also have an influence on the hereditary constitution of the sex cells. But the change in the latter, as a rule, will not correspond to the *somatsia* of the parents. There also occur simultaneous changes in the soma and the germ-plasm caused by one and the same external factor. One should not expect corresponding changes in this case either.

The next diagram illustrates the practical impossibility of parallel and somatic induction yielding corresponding changes in the germ-plasm

(figure 3).[7] Let the letter S stand for the soma, the letter K for the sex cells, and the letter R for the source of the influence from the external environment. In the case of parallel induction (I) there would be somatic changes (S_1) and sex cell changes (K_1) which would produce somatic changes (S_1) in the offspring identical to those found in the parent individuals. Since biological systems S and K differ quite strongly from one another there would be no basis for expecting them to respond equivalently to the same agent R.

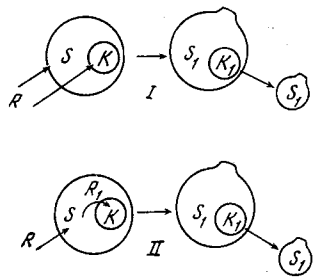

Figure 3. Diagram of parallel (I) and somatic (II) induction. Explanation in text.

The case of somatic induction (II in the diagram) would proceed as follows: the external agent (R) would act on the parent soma (S), which, upon changing, would affect the sex cells (K). The latter influence is indicated by the letter R_1. Thus the process results in an altered soma (S_1) and altered sex cells (K_1). The sex cells would be changed in such a way as to assure the emergence in offspring of the same changes as in the parents. If in parallel induction identical reactions by the soma and sex cells to the same influence (R) should be regarded as quite unlikely, then identical reactions are still less likely if one agent (R) acts upon the soma and another (R_1) acts upon the sex cells. The expression "identical reactions" is used here to simplify the discussion. In fact, a new trait should appear in the soma and a qualitatively different change should occur in the sex cells where the hereditary material must assure the emergence in the next generation of a somatic trait similar to the change in the parents. This clarification makes the possibility of an equivalent somatic induction seem even less likely.

The ideas introduced here are not new. They were expressed quite

[7] The diagram is published in the chapter "Dvizhushchie sily evoliutsii" ["Motive Forces of Evolution"], written by Leonid Ia. Blacher for a collectively reworked translation of A.F. Shell, *Obshchaia biologiia* [*General Biology*] pt. II (Moscow-Leningrad: 1933), p. 494. [The author is most likely referring to Aaron Franklin Shull, *Heredity* (New York: McGraw-Hill, 1926) which went through four editions between 1926 and 1948.] The diagram is reproduced in all editions of *A Course In General Biology* (see n. 6).

precisely at the beginning of the century by Detto. While considering the possibility of a transmission via the sex cells of changes caused in the soma by a mechanical influence, he noted that "in the case of irritation of the somatic cells by pressure, three processes occur: mechanical pressure, its influence on the protoplasm, and the irritation produced in the sex cell. The germ-plasm will experience a qualitatively different stimulus than the somata." Based on these considerations, Detto considered unfounded the idea that there could be equivalent changes in the soma and in the germ-plasm that had been subjected to the influence of that soma.[8]

In the next chapters we will examine some empirical attempts to demonstrate the possibility of the inheritance of acquired characters. A separate chapter is devoted to the work of Paul Kammerer, who strove long and determinedly, testing the influence of light, soil color, soil moisture, temperature, and certain other factors, to demonstrate such transmission by experimentation.

[8] Carl Detto, *Die Theorie*, (Chapter 9, n. 43), pp. 205–206.

CHAPTER 12

The Experiments of Paul Kammerer

The work of Paul Kammerer occupies a special place in the history of attempts to confirm experimentally the inheritance of acquired characters because of the variety of his experimental subjects and because of the consistency in his published results. Kammerer offered that consistency as indisputable proof of the inheritance of changes brought about by external influences.

In his historical study Guyénot gave a fully comprehensive survey and a quite objective evaluation of Kammerer's experiments. He prefaced his exposition of Kammerer's articles and books with a description of their general character. He noted above all that in the works of other authors who studied the inheritance of acquired traits the results were, as a rule, meager, inconsistent, and not very demonstrative. But with Kammerer there were no failures, no exceptions to the rule, and everything clearly followed the prediction of Lamarckian theory. In the reader's mind there should arise no doubts which Kammerer had not foreseen and refuted with theoretical arguments or the results of controlled experiments. "Anyone," wrote Guyénot, "who takes the trouble . . . to read carefully the 625 pages in octavo of Kammerer's works cannot fail to be amazed at the character of his writing. This is not an accurate exposition of experimental research accompanied by a discussion of the results and theoretical concepts. Taken as a whole, it reminds one more of a series of legal speeches made on behalf of the inheritance of acquired traits, in which the author from time to time reports certain experimental results. More often than not, however, the numbers are missing, the proportions are unknown, the protocol of the experiments is not reported. . . . One is left with a feeling of uneasiness and serious doubts as to the critical sense of the author who definitely represents an over-committed apostle of Lamarckism." [1] It was not surprising, concluded Guyénot, that Kammerer's research was met by an almost universal scepticism.

[1] Emil Guyénot, *La Variation et L'évolution,* vol. II, *L'évolution* (Paris: Gaston Doin, 1930), p. 64. [The modern reader should also be aware of the sympathetic, very readable but scientifically unsound account of Kammerer's research presented by Arthur Koestler in *The Case of the Midwife Toad* (New York: Random House, 1972). For critiques of Koestler's work see: Stephen Jay Gould, "Zealous Advocates," *Science,* 1972, *176:* 623-625 and Lester R. Aronson, "The Case of the *The Case of the Midwife Toad,*" *Behavior Genetics,* 1975, *5:* 115-125.]

In experiments concerning the influence of light on the cave-dwelling salamander, *Proteus,* Kammerer showed that when raised in the light and at a temperature higher than its natural environment *Proteus* changed from viviparity to oviparity, acquired a pigmented skin, and laid pigmented eggs. Strictly speaking, one could only conclude from this that the ability to change its pigment, genetically inherent in *Proteus,* is realized under the conditions of illumination and elevated temperature. As an example Kammerer referred to two slightly greyish individuals which were born to an uncolored female and a pigmented male. Guyénot remained highly skeptical of Kammerer's interpretation of this example, which attributed coloration in the offspring to the transmission of a trait acquired by their father.

Other experiments by Kammerer concerned the effects of light and heat on the structure of the eye of *Proteus.* The eyes of young individuals subjected to the influence of light grew to four times the normal size of the underdeveloped eyes characteristic of this amphibian. The crystalline lens did not degenerate, and the cornea, sclera, iris, and ciliary body differentiated along the pattern found in all salamanders living in the light. Kammerer did not report the details of these changes in the offspring of *Proteus;* the experiments therefore have no bearing on the question of the inheritance of acquired traits. Kammerer's interpretation of these experiments was that organisms which had lived in the dark for centuries had acquired new traits—viviparity, a reduction of skin pigment, and underdeveloped eyes. In his thinking, this prolonged experiment carried out by nature seemed to prove that the traits which arose under the influence of the living environment had become heritable. In the very first generation living under new conditions (illumination, elevation of temperature), however, *Proteus* became ovivivipparous, took on coloration, and acquired a normal eye structure. [2] "Is it possible," asked Guyénot, "to imagine more convincing proof that, despite a prolonged existence in the cold and darkness, through thousands of generations, the traits acquired under these conditions have not become hereditary? We are indebted to Kammerer for an excellent demonstration of the non-inheritance of acquired traits." [3]

Alexei N. Severtsov evaluated the results of Kammerer's experiments in exactly the same way as did Guyénot. "The supporters of Lamarck," he wrote, "usually accepted the idea that traits caused by exercise or lack of

[2] Paul Kammerer, "Experimente über Fortpflanzung, Farbe, Augen und Körperreduktion bei Proteus anguineus Laur. (Zugleich: Vererbung erzwungener Farbeveränderungen, III Mitteilung)," *Arch. Entw.-mech.,* 1912, *33:* 349-461.

[3] Guyénot (n. 1), p. 70.

exercise become inherited. It must be emphasized that Kammerer's experiments with *Proteus* eyes argue more readily against than in favor of such a view. When the eyes atrophy because of the absence of sufficient light, this trait in no way becomes fixed by inheritance, since under the influence of light stimulation the normal amphibian eye structure and function are reestablished. These facts might generally be taken as proof of the non-inheritance of traits which result from disuse."[4]

Kammerer also conducted experiments on the change in coloration of lizards under the influence of abnormal temperatures.[5] The white belly of the female *Lacerta muralis* became red (as in normal males) under these conditions. In *Lacerta fiumana,* where the males have a red and the females a yellow belly, the effect of cold was a whitening of the belly in both sexes, and the effect of heat was a whitening in males only. Crossing altered females with normal males, altered males with normal females, and altered males with altered females gave results resembling Mendelian segregation and allowed Kammerer to speak of the inheritance of changes brought about by temperature. In fact, Kammerer was obviously dealing not with varietal traits but with secondary sexual characters.

Kammerer's experiments which enjoy the greatest renown were those that examined the possibility of transmission of protective coloration in spotted salamanders that had been altered by the color and moisture of the soil on which they were raised. [Now] protective coloration is widespread in the animal kingdom, especially among insects and amphibians. Such protective coloration had already been explained for a long time by the theory of natural selection. Organisms which possess protective coloration, being less detectable by enemies, have a better chance of surviving than those which lack these traits. It was with these very traits that it was first demonstrated that natural selection was not simply a probable hypothesis but a fact accessible to experimental verification. Nonetheless Lamarckians continued to attempt to prove that phenomena of protective coloration arose under the direct influence of a colored background and that the protective trait which appeared during the individual's life became heritable.

At the beginning of the nineteen-twenties similar experiments were carried out by Bernhard Dürken and Leonora Brecher on pupae of the cabbage butterfly, by Aleksandr Petrovich Vladimirskii on the cabbage

[4]Alexei Nikolaevich Severtzov, *Etiudy po redyktsii organov pozvonochnykh zhivotnykh* [*Studies of Organ Reduction in Vertebrates*], in *Sobr. Soch.* [*Collected Works*], 1945, *3:* 501n.

[5]Paul Kammerer, "Vererbung erzwungener Farbeverändrungen, I u. II Mitteilung: Induktion von weiblichem Dimorphismus bei Lacerta muralis, von männlichem Dimorphismus bei Lacerta fiumana," *Arch. Entw.- mech.*, 1910, *29:* 456-498.

moth,[6] and by other investigators. Some of them succeeded in showing a change of coloration in insects which lived on a colored background or under filtered colored light; they also showed the inheritance of such traits. Dürken regarded his results as indisputable proof of the inheritance of acquired characters. Vladimirskii was much more cautious in his conclusions. He admitted that it was impossible to draw a final conclusion about the phenomena observed. "Do we have here the inheritance of acquired traits or the appearance of a sharp displacement in the norm of reaction that resulted from the selection of a particular hereditary variety? Could it be that the parent population was a hybrid with other varieties but that the selected variety gradually emerged and exhibited a different reaction to external influences than the parent population?"[7]

In Kammerer's coloration experiments, salamanders caught in the wild were placed on yellow clay (moist) or black garden soil (drier).[8] Living on a yellow background led, after three to four years, to an increase in the size of the yellow spots. The yellow spots that had existed at the beginning of the experiment merged with one another (the effect of the colored background), and new yellow spots appeared (the effect of increased moisture). When salamanders were raised on a black background, the black spots merged (the influence of the color of the background) and new black spots appeared (the effect of soil dryness). Larvae obtained from the salamanders with altered coloration were first raised on a neutral background which was gravel at the bottom of an aquarium. After metamorphosis,

[6]Leonore Brecher, "Die Puppenfärbung der Kohlweisslings, Pieris brassicae," [This volume contains three of seven parts of the author's complete monograph on the coloration of *Pieris brassicae,* see 1919, *45;* 1921, *48;* and 1922, *50* of *Arch f. Entw-mech.* for later parts.] *Arch. f. Entw.-mech.*, 1917-18, *43:* 88-221. Quoted according Bernhard Dürken, "Über die Wirkung färbigen Lichtes auf die Puppen des Kohlweisslings (Pieris brassicae) und das Verhalten der Nachkommen," *Arch. Entw-mech.*, 1923, [*54*]: 222-389. [Upon the death of Oscar Hertwig, the *Archiv f. Entwicklungsmechanik* absorbed Hertwig's *Archiv f. Mikroskopische Anatomie* under the editorship of Wilhelm Roux, with the assistance of Hermann Braus and Hans Spemann, What should have become volumes 53 and 54 for *Arch. f. Entwmech.* (1923-24) became, under a new composit title, volumes 98-104. This arrangement lasted until Roux's and Braus's deaths in 1924. Thereafter the journal was retitled *Wilhelm Roux's Archiv f. Entwichlungsmechanik* (1925, *105*). At the same time it became *Abteilung D* of the *Zeitschrift f. wiss. Biologie.* The seven volumes published during the years 1923-24 thus create a bibliographical headache. The correct citation above should read *Arch. f. mikr. Anat. u. Entw-mech.*, 1923, *99:* 222-389.] Aleksandr Petrovich Vladimirskii, "Über Vererbung experimentell erzeugter Färbigen von Puppen der Kohlmotte Plutella maculipennis," *Biol. Zbl.*, 1928, *48:* 739-59.

[7]Aleksandr Petrovich Vladimirskii, *Peredaiutsia li po nasledstvu priobretennye priznaki?* [*Are Acquired Traits Inherited?*] (Moscow-Leningrad, 1927), p. 134.

[8]Paul Kammerer, "Vererbung erzwungener Farbeveränderung. Iv Mitteilung: Das Farbkleid des Feuersalamanders (Salamandra maculosa Laurenti) in seiner Abhängigkeit von der Umwelt," *Arch. Entw.-mech.*, 1913, *36:* 4-193.

those young salamanders descended from parents that had become yellow were moved to a yellow background and those from parents that had become black were moved to a black background. The former became still yellower and their yellow spots even merged into two longitudinal stripes, a pattern which imitated the transition from the typical spotted salamander (*Salamandra maculosa f. typica*) to the striped salamander (*S. maculosa f. taeniata*). Similarly, the rearing of the offspring of the "black" salamanders on a black background led to a further increase in the amount of black pigment. In describing these experiments, Kammerer did not report the number of experimental animals nor the consistency of the results. When some of the offspring of the "yellow" parents were placed on a black background, the number of yellow spots and the symmetry of location of the spots decreased. Guyénot commented, "Reversing these transformations, when the descendants are placed in the opposite environment, they show that the traits displayed are not hereditary."[9] When some of the offspring of the "black" parents were placed on a yellow background, the spots merged into stripes, though these animals still remained less yellow than the offspring of the "yellow" parents. Guyénot would have considered this last observation as testimony in favor of the inheritance of color alterations in the salamander if the results cited had been accompanied by information about the number of experimental animals and if the described effect were reproducible.

According to Guyénot, the general conclusion to be gleaned from Kammerer's salamander experiments was the fact that the relative surface area of yellow or black coloring increased in successive generations in the presence of the continuing influence of one or another colored background. With a transfer from one environment to another, however, the previous coloration was reestablished, that is, the changes turned out not to be hereditary. Only the transformation from a row of spots to stripes showed a tendency to be inherited.

It was impossible to draw clear-cut conclusions from Kammerer's data. It was quite possible that the salamanders taken from nature were heterozygous and that their offspring displayed a segregation of traits. Guyénot, however, even regarded the altering effect of the colored background itself as quite doubtful. In nature very black, very yellow, and intermediately colored salamanders are found under one and the very same conditions of soil color. They mate freely with each other and thus indicate the genetic basis of the pigmentation differences. It is important to keep in mind that salamanders in nature are nocturnal animals which hide under rocks and fallen leaves during the day, so that the color of the soil would not likely have an effect on their coloration.

[9] Guyénot (n. 1), p. 79.

No one has repeated Kammerer's experiments exactly. Slavko Sećerov discovered that the larvae of salamanders raised on a yellow or a black background become correspondingly more yellow or more black.[10] Karl von Frisch observed similar results and considered them merely individual variations.[11] Curt Herbst used salamander larvae in an experiment to verify Kammerer's data.[12] He established that larval coloration changed in accordance with the color of the background, but that after metamorphosis the acquired traits were not preserved even if the young salamanders continued to be kept on the same background. Herbst's experiments, the results of which contradicted Kammerer's data, were more rigorously carried out. Successive changes of a given animal were followed and illustrated. Herbst's work forces one to doubt Kammerer's assertion of the specific progressive effect of the substrata color on the coloration of the animals. Yet the main reason that Kammerer's results remain unconvincing is that the genetic constitution of the experimental material he used was unknown. Kammerer failed to differentiate between individual adaptations and genetically conditioned differences in coloration. He interpreted as acquired those traits that, in fact, depended on the hereditary constitution of the various individuals.

Besides raising salamanders on different background colors, Kammerer carried out hybridization and gonad transplantation experiments. He first crossed the typical spotted form (*Salamandra maculosa f. typica*) with the striped form (*S. maculosa f. taeniata*) and found that the coloration of the latter was recessive. He also crossed the typical form with the striped form obtained by rearing *f. typica* on a yellow background (so-called *f. pseudotaeniata*). In the first and second generations the pattern had an intermediate character, but in succeeding ones it approached that of *f. typica*. Quantitative data on the area of the colored spots were not included in the work and the conclusions were based on the subjective visual perception of the author. Even in the second decade of the twentieth century such a method of studying the inheritance of quantitative traits would have been considered quite unsatisfactory. It is impossible to draw reliable conclusions from Kammerer's genetic experiments.

The goal of Kammerer's experiments with gonad transplants was to show the effect of the altered soma on the hereditary constitution. Kammerer transplanted ovaries from *f. typica* to *f. pseudotaeniata* and crossed

[10] Slavko Sećerov, "Über das Farbkleid von Feuersalamandern, deren Larven auf gelbem oder schwarzem Untergrunde gezogen waren," *Biol. Zbl.*, 1914, *34:* 339–344.

[11] Karl von Frisch, "Über den Einfluss der Bodenfarbe auf die Fleckenzeichnung der Feuersalamanders," *Biol. Zbl.*, 1920, *40:* 390–414.

[12] Curt Herbst, "Beiträge zur Entwicklungsphysiologie der Färbung und Zeichnung der Tiere. I. Der Einfluss gelber, weisser und schwarzer Umgebung auf die Zeichnung von Salamandra maculosa," *Abhandl. Heidelb Akad. Wiss.*, 1919, 7:64.

the female carrying the transplanted ovary with a male *f. typica*. Of two such crosses one produced nineteen offspring which had an asymmetrical pattern of spots typical of *f. typica* and forty-five offspring whose patterns resembled *f. pseudotaeniata*. The other cross produced nineteen offspring with the pattern typical of *f. typica* and fifty-four with a more or less clear symmetry of spots. Kammerer concluded that the altered soma of *f. pseudotaeniata* acted on the germ-plasm in the transplanted ovary cells of *f. typica*. It is interesting that in transplanting the ovaries from *f. typica* to a true *f. taeniata* the offspring retained the characteristics of *f. typica*. To interpret this difference in results, Kammerer used the ad hoc assumption that the soma of a long stabilized variety (*f. taeniata*) was not as active as the soma of a variety newly created by an environmental influence. The results of the cross of a male *f. typica* with a female *f. pseudotaeniata* carrying the ovaries of *f. typica* did not differ significantly from the results of the cross between a male *f. typica* and a female *f. pseudotaeniata*. The question arises whether the acclimatization of transplanted ovaries took place or whether offspring in this case developed from eggs from regenerated ovary cells of the recipient.

Kammerer foresaw this question, so he performed a hysterectomy on a female salamander without giving it an ovary transplant. This female remained infertile. Obviously, one such experiment does not eliminate the possibility of the regeneration of removed ovaries.[13]

In one of his later works Kammerer reported the results of an experiment on the ascidian *Cione intestinalis*.[14] The amputated siphons of this ascidian regenerate and the restored siphons turn out to be longer than normal. According to Kammerer the siphons were also lengthened in the offspring of the ascidians which had undergone the operation. Kammerer did not control all the variables of the experiment, and he based his conclusions on organ size without doing the required statistical analysis of his data.

Harold Munro Fox, who sought to verify these experiments of Kammerer, showed that the siphons of *Cione intestinalis* lengthen without regeneration, given a change in diet. If the ascidians were maintained under constant dietary conditions, the regeneration of siphons did not lead to their elongation.[15]

Kammerer also studied the changes in reproductive behavior and morphology of the midwife toad placed in altered living conditions.[16] When he maintained *Alytes* at an elevated temperature, Kammerer observed a shift from spawning on dry land to egg-laying in water. This resulted in the swelling of the egg strands so that the males could not wrap them around their back legs, that is, they could not fulfill their normal instinct to protect the offspring. Kammerer asserted that this change in behavior was transmitted by inheritance, that the offspring, even if returned to normal temperatures, continued to lay eggs in water. Upon crossing females that exhibited the altered reproductive behavior with normal males, these traits, according to Kammerer's data, were transmitted according to Mendelian laws: hybrids of the first generation all exhibited the normal behavior, while in the second generation segregation took place—individuals with normal and altered behavior appeared in a 3 : 1 ratio. For some reason the altered behavior seemed to dominate in reciprocal crosses. In an exposition of Kammerer's experiments, Guyénot noted that they were described without reference to the number of crosses and the number of offspring obtained, and without any specification of the genetic similarity of the material. It is known, for example, that there is a variety of *Alytes* which lives in the vicinity of Münster which normally lays its eggs in water. "Is it not possible," asked Guyénot, "that the high mortality of the animals in rearing them at a high temperature (which one does not learn about) entailed a selective elimination of some forms and a preservation of the forms homozygous for a recessive gene for reproduction in water, which trait was not manifest in the heterozygous parents?"[17]

Beginning with the third generation of the experimental toads, Kammerer noticed on the first finger of the foreleg the appearance of nuptial pads. These are normally lacking in the midwife toad but are characteristic for many frogs and toads which mate in water, since these pads facilitate the grasping of the female. In the fourth and fifth generations the pads enlarged and spread to the thumb and along the forearm to the elbow. Kammerer's sketches showing the histological cross-sections of these outgrowths of skin were not very precise. True dermal papillae present in the nuptial pads of frogs and toads were lacking here. According to Kammerer the pads were transmitted to the offspring raised at a normal temperature, and castration of males possessing the pads did not hinder their seasonal reappearance.[18] This is very strange, since it has been experimentally

[13] Experiments on the transplantation of sex glands to animals of a different genotype, meant to clarify the possibility of the influence of the soma on offspring which develop from another's germ cells, are presented in chapter 18. Such experiments by Kammerer are included in the present chapter so as not to interrupt the exposition of his works.

[14] Paul Kammerer, "Breeding Experiments on the Inheritance of Acquired Characters," *Nature*, 1923, *111:* 637–640.

[15] Harold Munro Fox, "Note on Kammerer's Experiments with 'Ciona' Concerning the Inheritance of an Acquired Character," *Journal of Genetics*, 1924, *14:* 89–91.

[16] Paul Kammerer, "Vererbung erzwungener Fortpflanzunsanpassungen. III Mitteilung. Die Nachkommen der nichtpflegenden Alytes obstetricans," *Arch. Entw.-mech.*, 1909, *28:* 447–545. [The first two parts of this monograph concern experiments with *Salamandra maculosa* and *S. atra*. They appear in *Arch. f. Entw-mech.*, 1907, *25:* 7–51.]

[17] Guyénot (n. 1), p. 87.

[18] Paul Kammerer, "Vererbung erzwungener Formveränderungen. I. Mitteilung: Die Brunftschwielen des Alytes-Männchen aus 'Wassereiern' (Zugleich: Vererbung erzwungener Fortpflanzungsanpassungen. V. Mittielung)," *Arch. Entw.-mech.*, 1919, *45:* 323–370.

shown in other frogs and toads, in particular in the yellow-bellied toad (*Bombinator pachypus*), which belongs to the same family as *Alytes,* that the formation of the nuptial pads depends on a spermatic hormone.

In 1923 William Bateson spoke on Kammerer's paper at the Linnaean Society and expressed doubt as to the reliability of the reported results. Bateson considered his sketches which illustrated Kammerer's articles of 1909 and 1910 unclear and unconvincing. Concerning the male *Alytes* used in Kammerer's presentation, Bateson noted that there was a black thickened patch on the elbows of this male but that under a magnifying lens the papilliary or spiny structures, characteristic of the nuptial calluses, were not visible. Furthermore, the formation which Kammerer took as the nuptial pad was located on the elbow and not on the dorsal and radial sides of the hand and fingers so that it could not facilitate the grasping of the female. Bateson therefore did not believe that the thickenings of skin described by Kammerer were nuptial pads.[19]

Ernest W. MacBride spoke in defense of Kammerer. He asserted that the structures in Kammerer's histological sections resembled those of amphibians which mate in water, particularly the grass frog. In the latter, however, the papilae and spines of the calluses were larger. Kammerer's work, in MacBride's words, "has yielded results which are of as much importance in the study of heredity from the evolutionary point of view, as all the Mendelian experiments taken together."[20] One can only imagine that this declaration not only failed to dissuade Kammerer's critics, but indeed gave rise to still further scepticism about his experimental results.

Bateson asked that he be given an opportunity to make a detailed study of the *Alytes* specimen demonstrated at the lecture. But Hans Przibram, the director of the Biological Institute in Vienna, refused to loan the specimen from the museum and suggested that someone study it at its present location. This suggestion was later accepted by G. Kingsley Noble, a famous American herpetologist from the American Museum of Natural History in New York. With Przibram's approval Noble published the results of his investigation.[21]

A single specimen was preserved in the Vienna museum as an illustration of Kammerer's experiments. This was the same specimen which Kammerer had shown during his presentation in England. Noble discovered on its hands neither nuptial calluses nor remnants thereof in the form of spines, bristles or other irregularities of the epidermis. On the back and palmar sides of the left hand a darkening was noted, which was less

[19] William Bateson, "Dr. Kammerer's Alytes," *Nature,* 1923, *111:* 738–739.

[20] Ernest William MacBride, "Dr. Kammerer's Experiments," *Nature,* 1923, *111: 841–842.* (Quotation is taken from the English.]

[21] G. Kingsley Noble and Hans Przibram, "Kammerer's Alytes," *Nature,* 1926, *118:* 209–211.

pronounced on the right hand. These spots gave the impression that a black foreign substance similar to India ink had been introduced. A study of the object under low magnification showed that it was not the epidermis which was colored, but the corium and the underlying muscles. Upon cutting the tissue, a black substance flowed out into the water in which the object was immersed. The preparation was poorly fixed, but nonetheless, with Przibram's permission, they succeeded in making histological sections, which confirmed the fact that the surface of the epidermis was smooth. The pigment substance was discovered in abundance in the corium and between the muscle fibers. Under high magnification it was evident that the substance had a granular character, and that these granules were black and not brownish-black like the granules of the melanin of amphibians. Grains of the substance did not give the reactions for melanin (loss of coloration in nitric acid and solubility in alkali). Controlled experiments with the introduction of India ink into many amphibians showed the same picture as the Kammerer specimen under study. Noble's general conclusions were that nuptial calluses or even their remnants did not exist on the specimen of *Alytes* he had investigated but that India ink had been injected under the skin of the forelegs.

Following Noble's report, Przibram published a note in the same journal issue. It began with the words, "It is clear from the foregoing account that the only one of Kammerer's experimentally modified *Alytes* still preserved cannot in its present state be regarded as a valid proof of the nuptial pads artificially produced in this species."[22] Citing letters he had received, Przibram asserted further that the photographs showing the irregularity of the epidermis described by Kammerer as nuptial calluses were not retouched. Consequently, these irregularities had existed, but became undetectable due to damage caused by the transport of the specimen from Vienna to England and back. Concerning the indisputably established presence of India ink in the tissues of the forelegs of the object under study, Przibram allowed the possibility that "some one has tried to preserve the aspect of such black nuptial pads in fear of their vanishing by the destruction of the melanin through exposure to the sun in the museum by injecting the specimen with India ink." Przibram further testified that Kammerer was completely surprised by the results reported by Noble and gave his permission for a chemical investigation of his specimen. In a letter to Przibram of 18 February 1926, Kammerer offered the suggestion that someone had intentionally made such an injection in order to cause trouble for him. He noted, however, that the black pigment was found in the same place as it had occurred in the living animal.[23]

[22] *Ibid.,* p. 210.

[23] *Ibid.,* p. 211.

It must be noted that even the authors who did not share his views on the inheritance of acquired characters did not ascribe to Kammerer a conscious intention to mislead anyone. Harry Federley,[24] Guyénot,[25] and Richard B. Goldschmidt[26] confined themselves to expressions of bewilderment.

I describe here this episode of Kammerer's career more or less in detail not to put his scientific integrity in doubt but to provide corrections for the reports of those active supporters of the inheritance of acquired characters who later wrote about these events.[27]

[24] Harry Federley, "Weshalb lehnt die Genetik die Annahme einer Vererbung erworbener Eigenschaften ab?" *Z. indukt. Abstammungs- und Vererbungslehre*, 1930, *54:* 20–43.

[25] Guyénot (n. 1), pp. 63–65.

[26] Richard Benedict Goldschmidt, *In and Out of the Ivory Tower; The Autobiography of Richard B. Goldschmidt* (Seattle: University of Washington Press, 1960).

[27] Petr O. Sakharov, *Nasledovanie priobretaemykh svoistv* [*The Inheritance of Acquirable Characters*] (Moscow: 1952), pp. 207–208. N.I. Feiginson, *Nasledovanie priobretaemykh svoistv* [*The Inheritance of Acquirable Characters*] (Moscow: 1951), pp. 13–14. I.M. Poliakov, *O nasledovanii priobretaemykh svoistv* [*On the Inheritance of Acquirable Characters*] (Moscow: 1951), p. 25.

CHAPTER 13

Are the Results of Mechanical Influences Inherited?

We described in chapter seven experiments which showed that the amputation of the tail of mice and rats did not lead to the inheritance of that injury. In the second half of the nineteenth century an attempt was made to discover an inheritance of changes caused by mechanical action on the central or peripheral nervous system. The investigations of Charles E. Brown-Séquard, published from 1850 to 1892, attracted a good deal of attention. His results were sometimes regarded as persuasive evidence in favor of the inheritance of acquired traits.[1] Brown-Séquard severed the sciatic nerve in guinea pigs, cut the right or left half of the spinal cord transversely, or severed only the lateral or anterior columns. The experimental animals then displayed epileptic-like seizures. According to his data, the offspring of these guinea pigs sometimes displayed epileptic seizures and certain morphological changes, such as impairment in the development of eyes, ears, and toes of the hind legs.

Brown-Séquard's experiments were repeated from time to time by various authors. George John Romanes was particularly persistent in this matter. In a two-volume work published posthumously, *Darwin and Post-Darwinism,*[2] he dealt in detail with the theoretical assumptions, peripheral arguments, and experimental results offered in support of the inheritance of acquired traits. He also presented the ideas and facts testifying against such inheritance. Over the course of twenty years Romanes himself attempted to reproduce the experimental results of Brown-Séquard. Although he did not succeed in obtaining conclusive results, this did not keep him from retaining a Lamarckian inclination in his interpretation of evolution.

[1] It is possible to point out certain articles by this author: Charles-Édouard Brown-Séquard, "Remarques sur l'épilepsie causée par la sciatique chez les cobayes," *Arch. physiol. norm. et pathol.*, 1870, *3:* 153–160; "Quelques faits nouveaux relatifs à l'épilepsie qu'on observe à la suite de divers lésions du système nerveux, *ibid.*, 1871–1872, *4:* 116–120. [For the most convenient English summary of this work see Brown-Séquard, "On the Hereditary Transmission of Effects of Certain Injuries to the Nervous System," *Lancet*, 1875, *1:* 7–8.]

[2] George John Romanes, *Darwin, and after Darwin. An Exposition of the Darwinian Theory and a Discussion of Post-Darwinian Questions*, 2 vols. (Chicago: Open Court, 1892–95). [Blacher refers to the 1895 German edition of this work.]

In a discussion of the experiments of Brown-Séquard and his followers, Guyénot directed attention first of all to the inadequacy of the descriptions in their publications.[3] All the works he examined failed to mention the variety of guinea pigs, the purity of their breed, and the number of generations investigated. For instance, in 1890 B.S. Dupuy, a pupil of Brown-Séquard, described experiments performed many years earlier. He mentioned that among seven generations of descendants of parents in which the sciatic nerve had been severed, one guinea pig displayed an underdeveloped hind leg; among the offspring of parents with a severed cervical sympathetic nerve, one animal possessed asymmetrical facial features.[4] Just as unconvincing were the data of C. Westphal (1871). After severing the sciatic nerve in the spinal cord of guinea pigs, he observed epileptic phenomena in two of the offspring of one of the experimental females. Heinrich Obersteiner, who investigated thirty-two offspring of parents with a severed sciatic nerve, found that only two exhibited the trait of epilepsy and a few had impaired eye development.[5] Other investigators were not able to confirm the Brown-Séquard data at all. M. Sommer observed epileptic phenomena after severing of the sciatic nerve in forty guinea pigs, but not one of the offspring displayed epilepsy or any kind of morphological anomaly.[6] Similarly, A.E. Taft did not observe seizures in one hundred fourteen offspring of guinea pigs with experimentally induced epilepsy.[7] A. Maciesza and A. Wrzosek either tightly constricted the sciatic nerve with a ligature, severed the nerve, or cut a part of it out; subsequently they observed epileptic phenomena in the post-operative animals.[8] Thirty-three displayed certain signs of epilepsy, though in almost half of the control animals similar phenomena also appeared. According to the data of these authors, morphological anomalies arose spontaneously in 1-2% of the guinea pigs, that is, just as frequently as in the offspring of the traumatized guinea pigs in Brown-Séquard's experiments. Guyénot noted further that in a superficial observation it is easy to confuse mild displays of epilepsy with reflex movements of scratching in the hind legs.

In summarizing his discussion of Brown-Séquard's work and subsequent attempts to verify these investigations, Guyénot regarded all the data as "an interpretation of accidental coincidences mixed with fantasy. The author kept only the positive cases, without critically examining them. He systematically neglected the negative results, which were much more numerous: thus prejudices are born."[9]

[3] Emil Guyénot, *La variation et l'évolution*, vol. II, *L'évolution*, pp. 42-45.

[4] Guyénot, *ibid.*, p. 42.

[5] Heinrich Obersteiner, "Zur Frage der hereditären Übertragbarkeit acquirierter pathologischer Zustände," *Neurol. Cbl.*, 1900, *19:* 498-499.

[6] M. Sommer, "Die Brown-Séquard'sche Meerschweinchenepilepsie und ihre erbliche Übertragung auf die Nachkommen," *Beitr. zur pathol. Anat. u. allg. Pathol.*, 1900, *27:* 291-330.

[7] Guyénot (n. 3), p. 44.

[8] A. Maciesza and A. Wrzosek, "Experimentelle Untersuchungen über die durch Ischiadicusverletzung hervorgerufenen Brown-Séquard'sche Meerschweinchenepilepsie," *Arch. Rassen- u. Gesellschaftsbiologie*, 1911, *8:* 1-24, 145-163; A. Wrzosek and A. Maciesza, "Über die Entstehung, den Verlauf und die Vererbung der durch Rückenmarksverletzungen hervorgerufenen Meerschweinchenepilepsie," *ibid.*, 1914-15, *11:* 290-298.

Ilya Ilich Mechnikov discussed the possibility of the inheritance of mechanically induced injuries in his theoretical works. In an earlier period he merely voiced the opinion that "changes obtained as the result of an operation such as the amputation of the tail of dogs are sometimes inherited."[10] Later Mechnikov significantly changed his attitude towards these arguments that favored the inheritance of injuries. "In former times," he wrote, "when science assumed that acquired traits were easily inherited, we used to ask ourselves why the hymen, which had developed over the course of many generations, did not show the slightest signs of disappearing. This example was one of many which further shook the theory of the transmission to offspring of traits acquired in the course of an individual life."[11]

We have already discussed in chapter seven the purely hypothetical idea that the custom of squatting among some peoples leads to a change in the skeletal structure of their lower extremities. Citing his personal observations, pedagogue Jean Piaget wrote about the possible significance of muscular exertions on changes in organisms. He investigated more than eighty thousand specimens of *Limnaea stagnalis* from Lac de Neuchâtel during a period from 1919 to 1929. This fresh water snail, which usually lives in still or slowly moving water, settles in rocky shallows in alpine lakes where the waves force it to secure itself to the rocks. In the forms found in rough-water environs the foot is broader and the shell is correspondingly shorter and has a wider opening than in forms from quiet bodies of water. Piaget showed that by maintaining the newly hatched snails in a shaking container the rough-water variations were experimentally reproduced but were not transmitted to the offspring. Nonetheless, Franck Bourdier considered Piaget's observation as testimony in favor of Lamarckism. He suggested that the inheritance of acquired traits is realized only after a centuries-long influence by a mechanical factor. Bourdier introduced no arguments other than subjective convictions to support his suggestion.[12]

We should also mention experimental works that, to judge from their

[9] Guyénot (n. 3), p. 57.

[10] Ilya Ilich Mechnikov, "Ocherk voprosa o proiskhozhdenii vidov" [Essay on the Question of the Origin of Species"] (1876), *Izbr. biol. proizv.* [*Selected Works in Biology*] (1950), p. 91.

[11] Ilya Ilich Mechnikov, *Etiudy o prirode cheloveka* [*Studies on the Nature of Man*] (1903; Moscow: 1923), pp. 64-65.

[12] Jean Piaget, *Biologie et connaissance* (Paris: 1967). In this book Piaget makes reference to his earlier published works. He is cited here according to Franck Bourdier, "Le Lamarckisme et la raison," *Cahiers rationalistes*, 1967; *no. 252.*

titles, contain proof of the inheritance of changes caused by the exercise of organs. Among these is W.R. Bloor's article "The heritable effect of exercise on the phospholipid and cholesterol content of muscle." [13] Bloor forced female rats to run for a month or more. When their offspring reached adulthood, he exercised those rats in a similar fashion. He analyzed muscle tissue of some of the experimental rats for phospholipid and cholesterol content, and bred the remaining rats. Third generation daughters were also exercised for one to two months and their muscles analyzed. It was established that the muscles of all the rats which had exercised were characterized by an increased phospholipid and cholesterol content. Of course, one could speak about the inheritance of such exercised-induced changes only if a higher level of phospholipid and cholesterol were found in the offspring of active rats who were themselves not forced into prolonged activity. Bloor's experiments show only that in each generation the chemical composition of the muscles changes in a definite way. But it is impossible to draw from his work any conclusions concerning the inheritance of these changes.

Among animal breeders there is a widespread belief that the high milk yield of cattle is due to the constant mechanical stimulation to the teats during milking and that the results of this action seem to effect not only the individuals experiencing the mechanical influence but their offspring as well. Since a physiological or genetic mechanism for such an effect through the teats on the germ cells and thereby on the milk production of the offspring was inconceivable, the breeders tried to think up some other explanation for the inheritance of a high milk yield. E. Dechambre advanced one such hypothesis. [14] He believed that the state of neoteny—the absence of metamorphosis and the consequent occurrence of sexual maturity in the larval stage as found with some salamanders, such as the axolotl—was linked to the underdevelopment of the thyroid gland. Since the larvae of the axolotl (*Amblystoma mexicanum*) live in nature under the same ecological conditions as the larvae of another species, *A. tigrinum,* which nonetheless undergoes metamorphosis, Dechambre suggested that this underdevelopment was the consequence of some kind of environmental influence. For some reason, however, Dechambre considered neoteny in the axolotl as a trait acquired under the influence of the environment and transmitted through inheritance. He concluded that this was an example of the environment acting on the soma which in turn affected the germ-plasm by means of hormones. In Dechambre's opinion, one could reason analogously that the intensified functioning of the milk glands

[13] W.R. Bloor, "Inheritance Effect of Exercise on the Phospholipid and Cholesterol Content of Muscle," *Journal of Biological Chemistry,* 1940, *132:* 77–82.

[14] E. Dechambre, "Réflexions sur les caractères acquis et sur leur transmissibilité," *Rev. gén. Sci. pures et appl. et Bull. Soc. philomat.,* 1949, *56:* 182.

during milking affected the production of hormones, which in turn acted upon the germ-plasm and caused a still more intensified development of the milk glands in the offspring. Of course, Dechambre could not cite any direct corroborating evidence for this hypothesis. He invented it simply to refute the Darwinian explanation, that is, the idea that the milk yield in cattle increased as a result of the artificial selection of favorable hereditary changes. [15]

[15] Long before Dechambre, Serebrovskii made critical statements concerning the possibility of increasing milk yield by the increase in milking (see chapter 10).

CHAPTER 14

Are the Results of the Influence of Temperature Inherited?

In summaries of the literature which list only arguments in favor of the inheritance of acquired traits, much attention is devoted to experiments involving the influence of an abnormal temperature on cold-blooded animals, particularly insects. Max Standfuss published works of this sort between 1894 and 1902.[1] He exposed caterpillars of the thistle butterfly (*Vanessa urticae*) to temperatures below 0°C. In his experiments a total of 8,231 caterpillars formed chrysalises, and forty-two (0.5%) of the butterflies from these were darker than normal. By inbreeding the butterflies he obtained five hundred forty-five chrysalises. Out of forty-two chrysalises derived from the most darkened butterflies only four melanic butterflies emerged, and of these only one was as dark as the parent form changed by the direct action of the cooler temperature. "What is the significance this unique melanic butterfly?" asked Guyénot, "Is it a mutation? Does it represent an atavistic resurgence? It is impossible to determine. The experiment is faulty in conception since the genetic constitution of the parents is unknown."[2]

Emil Fischer, repeating Standfuss's experiment, obtained approximately 5% noticeably darkened individuals among the offspring of dark thistle butterflies which had emerged from cooled chrysalises.[3] Fischer performed analogous experiments on the tiger moth, *Arctia caja*. He cooled the chrysalises to −8°C. Out of forty-one more or less noticeably darkened moths one particularly dark male appeared. He was mated with a less dark female which then produced one hundred seventy-three normally colored moths, seventeen more or less dark, and only two close to the coloration of the father. "Fischer," noted Guyénot, "considered that his experiments offered decisive proof of the inheritance of acquired traits. It is obvious

[1]Max Standfuss, "Zur Frage der Gestaltung und Vererbung auf Grund 28-jähriger Experimente," *Insektenbörse*, 1902, *19*. Cited according to Hans Przibram, *Experimental-Zoologie*. Vol. 3. *Phylogenese inklusive Heredität* (Leipzig u. Wien: Franz Deuticke, 1910).

[2]Emil Guyénot, *La variation et l'évolution*. vol. 2. *L'évolution*, p. 57.

[3]Emil Fischer, "Experimentelle Untersuchungen über die Vererbung erworbener Eigenschaften," *Illustr. Z. Entomol.*, 1901, *6*: 49–51, 363–381.

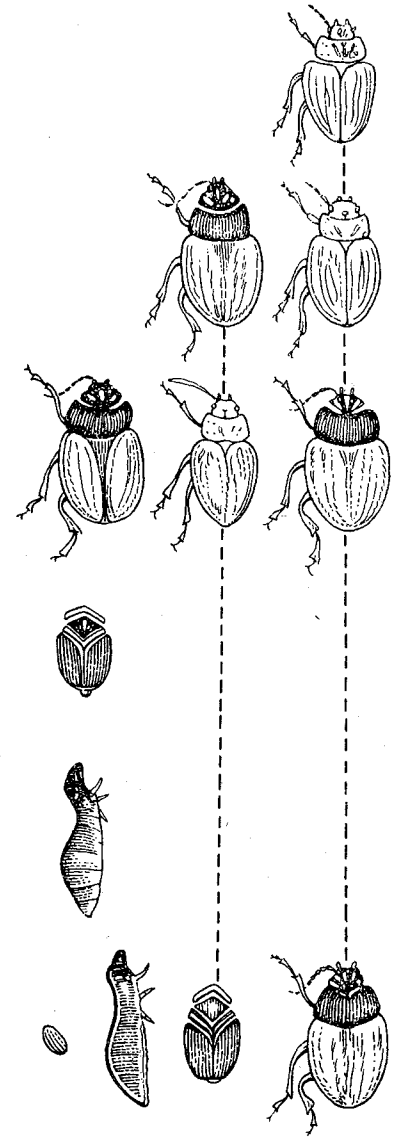

Figure 4. Diagram of Tower's experiment (according to Yurii A. Filipchenko).

Each vertical column represents the effect of heating different developmental stages of the beetle. From left to right: heating the egg or larva—an absence of change; heating the chrysalis—nonheritable lightening of the emerging beetles; heating the beetle during maturation of the sex cells—a change in its offspring.

they in no way meet the standards of a properly conducted experiment."[4]

In discussing the data obtained in the experiments of Standfuss and Fischer, Mikhail M. Zavadovskii suggested that temperature influenced the germ cells directly, not through somatic induction. He declared that no definite conclusions could be made on the basis of these experiments,

[4]Guyénot (n. 2), p. 57.

"since the tests were conducted on genetically unknown material and the inheritance was traced through only one generation." [5]

The possibility that temperature acts directly on the hereditary substance of the germ cells is clear from the widely quoted investigations of William L. Tower on the Colorado potato beetle. [6] Tower set up his experiment in the following manner (figure 4).

He subjected either the deposited eggs, the larvae, the chrysalises, or the newly emergent beetles to an elevated temperature. In some series of the experiments he found that the color of the thoracic corselet and elytron of the beetles became lighter. The essence of his findings was as follows: when heat was applied to the eggs or the larvae, no change occurred in the adult coloration; when heat was applied to the chrysalises, the adult beetles exhibited a lightening in color but their offspring possessed normal coloration. Finally, when heat was applied to already hatched beetles, at a time when the germ cells were maturing, the beetles themselves did not change but their offspring were lighter colored and this altered trait persisted in succeeding generations. The crossing of such light colored beetles with normal ones showed that the new trait was recessive, since hybrids of the first generation were darkly colored, while the second generation exhibited a segregation of traits, with 75% dark and 25% light colored individuals. Thus, when heat was applied to chrysalises, it produced nonheritable phenotypic changes. This phenomenon fits group 4 in Guyénot's classification scheme and group A_1 in Zavadovskii's diagram (see chapter eleven). When heat was applied to adult beetles during the maturation of their germ cells at a time when the hereditary substance seemed sensitive to heating, the heated beetles themselves did not change, that is, a new trait was not acquired in the course of the individual life, but changes arose in the germ cells which were expressed as an altered trait in succeeding generations. This phenomenon fits group 13 in Guyénot's scheme and group C in Zavadovskii's diagram. Not one of Tower's experiments can serve as evidence for the inheritance of acquired traits.

Petr Aleksandrovich Kosminskii described in a series of works the influence of temperature on the development of willow silkworm moths (*Stilpnotia salicis*). With a comparatively mild cooling of the chrysalises, he obtained various morphological changes, such as altered size, shape, and venation pattern of the wings. At first Kosminskii did not notice altered traits in the offspring of the cooled moths. [7] Later he established that the

[5] Mikhail Mikhyalovich Zavadovskii, *Dinamika razvitiia organizma* [*Dynamics of the Development of the Organism*] (Moscow: 1931), p. 417.

[6] William Lawrence Tower, *An Investigation of Evolution in Chrysomelid Beetles of the Genus "Leptinotarsa," Carnegie Institution of Washington. Publication no. 48,* (Washington, D.C.: 1906), 320 p.

[7] Petr Aleksandrovich Kosminskii, "Izmeneniia morfologicheskikh svoistv u babochek pod

females whose wing venation pattern had not changed as a result of the cooling nevertheless had offspring with altered venation (28% in the first generation, 33% in the second). [8] Kosminskii considered his experiments as evidence of the altering effect of cooling on the germ cells (germ-plasm). In general, the results of Kosminskii's experiments are similar to those obtained by Tower; they cannot serve as evidence for the inheritance of acquired traits.

M. Willy Gerschler and later Harry Federley came to the conclusion that the majority of results obtained in temperature experiments on butterflies did not depend on the altering effect of lowered temperature. [9,10] Using the dark butterflies which appeared in the experiments for mating, the investigators effected a selection of the corresponding genotype, which happens in nature independent of any experimental influences. Federley himself demonstrated such a selection on the butterfly *Leucodonta bicoloria.*

"All these experiments," wrote Guyénot, "carried out in an era when it was not even suspected that organisms could carry a large number of latent genetic factors, possess only an historical interest." [11] One can agree with Guyénot's assertion if the word "only" is excluded from it. The abovementioned experiments of Standfuss, along with many similar ones, have not only a substantial historical but also a methodological significance. They serve to demonstrate how and how not to set up an experiment to test for the inheritance of acquired traits.

Experiments to determine whether the effects of abnormal temperatures are inherited were also carried out on warm-blooded animals. Francis Bertody Sumner subjected mice of an unknown hereditary constitution to an elevated temperature (around 26°C) and obtained in them an enlargement of the tail and feet. These changes were also displayed in a portion of their offspring raised at a normal temperature. The results did not

vliianiem terperatury" ["Changes in Morphological Features in Butterflies Under the Influence of Temperature"]. *Dnevnik Zool. otd. Ob-va liubit. estestvozn., antropol. i etnogr.* [*Journal of the Zoological Section of the Society of Amateurs in Natural Science, Anthropology and Ethnography*], 1913, *1:* 121–134; "K voprosu o nasledovanii priobretennykh svoistv u babochek" ["On the Question of the Inheritance of Acquired Traits in Butterflies"], *ibid.*, 1915, *2:* 176–181.

[8] Petr Aleksandrovich Kosminskii, "Opyty nad nasledovaniem izmenenii, poluchennykh pod viliianiem temperatury na zarodyshevuiu plazmu" ["Experiments on the Inheritance of Changes Obtained Through the Influence of Temperature on the Germ-Plasm"], *Russkii zoologicheskii zhurnal* [*Russian Journal of Zoology*], 1923, *3* and *4:* 284–294.

[9] M. Willy Gerschler, "Melanismus bei Lepidopteren als Mutation und individuelle Variation," *Z. indukt.* Abstammungs- und Vererbungslehre, 1915, *13:* 58–87.

[10] Harry Federley, "Die Bedeutung der polymeren Faktoren für die Zeichnung der Lepidopteren," *Hereditas*, 1920, *1:* 221–269.

[11] Guyénot (n. 2), pp. 59–60.

specify the duration of exposure to elevated temperature, and Sumner observed attenuation as well as enlargement of body parts in the offspring. Sumner himself did not consider these experiments as proof of the inheritance of acquired traits.[12]

Subjecting rats to an elevated temperature, Hans Przibram obtained a change in their tail length. In the second generation, however, the trait had already not only returned to normal, but gave results opposite to those obtained in the F_1 generation.[13]

[12] Francis Bertody Sumner, "The Reappearance in the Offspring of Artificially Produced Parental Modifications," *Amer. Naturalist,* 1910, *44:* 5-18; "An Experimental Study of Somatic Modifications and their Reappearance in the Offspring, pt. 2" *Arch. Entw. mech.,* 1910, *30;* 317-348. "Some Studies of Environmental Influence, Heredity, Correlation and Growth in White Mouse," *J. Exp. Zool.,* 1915, *18:* 325-432.

[13] Hans Przibram, "Die Schwanzlänge der Nachkommen temperaturmodifizierter Ratten, Mus (Epymis) decumanus Pall. und (E.) rattus L.," *Arch. mikr. Anat. und Entw.-mech.,* 1925, *104:* 548-610 (see chapter 12, n.6)

CHAPTER 15

Can Changes Caused by Diet be Inherited?

A. Pictet fed caterpillars of the unpaired silkworm (*Ocneria dispar*) hazelnut leaves in place of their normal food oak leaves.[1] The moths retained a paler than normal coloration for two generations. At first glance it seemed that Pictet had succeeded in demonstrating the inheritance of acquired coloration. One might even have expected that the acquired traits would become more firmly fixed if the feeding with the unaccustomed food had been continued for several generations, that is, if one introduced those factors—prolongation and repetition of the influence—which the Lamarckians insisted were necessary. But this expectation was not realized. When Pictet repeated his experiment through four generations it turned out that the pale coloration which had appeared in the first generation and was retained in the second and third disappeared entirely in the fourth despite continued provision of the unaccustomed food. The very title of his later work, "Investigations demonstrating the noninheritance of acquired traits,"[2] reflect Pictet's attitude toward the results obtained.

Over the course of the past fifty years a large number of dark varieties of local butterfly species have been discovered in areas, particularly in England, where factory and industrial smoke has polluted the atmosphere. In 1924 J.B.S. Haldane conclusively proved the reality of this phenomenon, which received the name industrial melanism.[3] J.W. Heslop-Harrison and F.C. Garett attempted to explain it.[4] They suggested that darkening in the butterflies depended on the fact that the caterpillars fed on leaves covered with tiny particles of mineral sediment from the air. They fed the caterpillars of the inchworm *Selenia bilunaria* the leaves of hawthorns whose branches had previously stood in a weak solution of manganese sulphide or lead nitrate. A certain percentage of the moths developing from these

[1] Arnold Pictet, "Influence de l'alimentation et la humidité sur les variations des papillons," *Mem. Soc. Geneve,* 1905, *35:* 45-128.

[2] Arnold Pictet, "Recherches demontrant la non-hérédité des caractères acquis," *Compt. Rend. Soc. phys. et hist. natur.,* 1920, *37:* 24-28.

[3] J.B.S. Haldane, *Evolution as Process* (London: 1954).

[4] J.W. Heslop-Harrison and F.C. Garett, "The Induction of Melanism in the Lepidoptera and its Subsequent Inheritance," *Proc. Roy. Soc. London,* Sect. B. 1926, *99:* 241-263.

caterpillars (4% in one experiment, as much as 16% in another) displayed changes similar to the industrial melanism observed in nature. Harrison obtained a similar effect by feeding the caterpillars of another inchworm, *Thephrosia bistortata*, leaves taken from trees in highly polluted regions.[5] The crosses between such dark females and normal, light-colored males revealed the recessive nature of these melanic changes. It was not ruled out that the salts might have a mutagenic effect. Recently, however, the works of H.B.D. Kettlewell gave a satisfactory solution to the whole problem.[6] This author showed that industrial melanism was a result of the external environment acting not on changes in separate individuals but on the genetic make-up of the population. Near factories smoke particles polluted the atmosphere, grass, and leaves of trees. Dark moths gained an advantage over light-colored ones since they were less noticeable to insectivorous birds. The consequence was the natural selection and survival of the melanic forms. Among the dark moths there were both individual, nonheritable deviations from normal colorations and melanic mutations. The survival of the former affects the make-up of the population at any given moment, but the character of future generations depends on the presence of the latter.

At one time it was suggested that one way to cause hereditary change through assimilation of an abnormal substance would be a partial exchange of albumin between bird eggs of different varieties, species, or even orders. Sergei Ivanovich Bogoliubskii began experiments of this type, but they yielded very unclear results.[7] He introduced albumin from New Hampshire chicken eggs into the eggs of Leghorn chickens for three generations. He obtained a certain percentage of individuals with pale-yellow feathers, which are known to occur normally in certain varieties of Leghorns. Among reports which subsequently appeared in print, some confirmed, though vaguely,[8] and others refuted the possibility of the

[5] J.W. Heslop-Harrison, "The Inheritance of Wing Colour and Pattern in the Lepidopterous Genus Thephrosia. II. Experiments Involving Melanic Thephrosia bistortata and Typical Thephrosia crepuscularia," *J. of Genetics*, 1926, *17:* 1–9.

[6] Henry Bernard Davis Kettlewell, "Selection Experiments in Industrial Melanism in Lepidoptera," *Heredity*, 1955, *9:* 324–342; "Industrial Melanism in Moths and its Contribution to Our Knowledge of Evolution," *Proceedings of the Royal Institute of Great Britain*, 1967, *36:* 616–635.

[7] Sergei Ivanovich Bogoliubskii, "Vliianie na postembrional'noe razvitie zhivotnykh izmenennogo embrional'nogo pitaniia" ["The Effect of Altered Embryonic Nourishment on Animals' Postembryonic Development"], *Trudy Pushkinskoi nauchnoi-issledovatel'noi laboratorii razvedeniia c.-x. zhiv.* [*Works of the Pushkin Scientific Research Laboratory for Breeding of Agricultural Animals*], 1949, *no. 3:* 7–16; "Vliianie zamenu belka v inkubiruemykh iaitsakh na okrasku opereniia kur i potomstva ikh" ["The Effect of Albumin Exchange in Incubated Eggs on Feather Coloration in Chickens and Their Offspring"], *ibid.*, 1952, *no. 3:* 88–93.

[8] G.A. Mashtaler, "Vliianie chuzherodnogo iaichnogo belka na razvitie ptitsy" ["The

inheritance of characters acquired through the influence of foreign egg albumin.[9] The results of the work of E. Letard and P. Szumowski were particularly striking. In their experiment they used ninety eggs of five different breeds of chicken, viz., Sussex, Cuckoo de Malines, Black Bress, White Leghorn, and Rhode Island Red. They performed exchanges of from two to four mililiters of albumin. Twenty chicks died before hatching, sixteen hatched, and two "hybrids" (a Leghorn and a Rhode Island) lived to nine months of age. The coloring of the feathers, beak, and tarsometatarsis did not differ in a single case from the existing traits of purebred chickens.[10] In 1956 in a paper read at an international genetics symposium in Tokyo, Khila Faivilovich Kushner presented, without criticism, data concerning the exchange of albumin in bird eggs as a "means of changing heredity." This paper, which was published in Russian in the journal *Agrobiologiia*, referred to an unpublished work by L. Angelov, who had, according to Kushner, "introduced albumin extracted from the eggs of eagles, geese, and turkeys into the eggs of Leghorn and Rhode Island chickens, and observed in all variations a number of morphological changes in the offspring."[11] Reference was made in the text to a drawing which portrayed a female condor from whose eggs albumin was taken and introduced into a chicken egg. (Speaking of albumin from the eggs of an eagle, Angelov and Kushner evidently had this condor in mind, unmindful of the fact that the condor belongs to the suborder *Cathartae* and the eagles to the suborder *Falcones* in the order of predatory birds.) The unusual success of Angelov, who obtained positive results in literally "all variations" of his experiment, obliges one to regard his report with particular caution.

The occurrence of polymorphism in social insects was explained by some authors as an effect of food on the emergence of new hereditary traits. Armen Levonovich Takhtadzhan wrote vividly about such fantasies. "How could their [the worker bees'—L.B.] numerous and very complex adaptations have arisen by way of a direct adaptation if they cannot at all reproduce and thereby transmit their acquired traits to their offspring? None of the Lamarckians . . . has yet given an intelligible answer to this

Effect of Foreign Egg Albumin on the Development of Birds"], *Doklady Akademii Nauk SSSR Papers of the Academy of Science of the USSR*, 1950, *71:* 549–552.

[9] J.L. Churý and R. Švec, "Vegetative Hybridization in Animals," *Animal Breeding Abstracts*, 1955, *23*, No. 2: 189; Z. Kaminskii, O. Kardymowicz, Z. Piotrowicz, and Z. Zebracka-Szczesna, "Experiment on the Effect of Interchange of Egg White in Poultry Eggs on the Offspring," *Animal Breeding Abstracts*, 1956, *24*, no. 1: 62.

[10] E. Letard and P. Szumowski, "On So-Called 'Vegetative Hybridization' in Poultry," *Animal Breeding Abstracts*, 1955, *23*, no. 1.

[11] Khila Faivilovich Kushner. "Vliianie metabolicheskikh faktorov na nasledstvennost' zhivotnykh" ["The Effect of Metabolic Factors on the Heredity of Animals"], *Agrobiologiia* [*Agrobiology*], 1957, *no. 1:* 19–35.

question. One must not accept the suggestion, absolutely monstrous in its absurdity, that the transfer of hereditary traits to worker bees occurs through food. Such statement goes too far beyond the limits of scientific knowledge. The very possibility of such an explanation graphically shows the full extent of the theoretical unsoundness of contemporary Lamarckism."[12] From the excerpt cited, it is not clear whether Takhtadzhan knew that such a suggestion had in fact been offered in print. In one article, however, the authors asserted that the morphological traits and the building instincts of the worker bee, formed through the exercise of some parts of the body and the disuse of other parts, were transmitted by means of milky secretion of the feeding glands of the worker bees. Workers fed this secretion to the larvae of the queen bees and drones. The two latter did not themselves acquire the traits of the worker bee but apparently transmitted them to the worker bees of the next generation.[13]

E.S. Smirnov and his co-workers published several works in which they made yet another attempt to prove the inheritance of changes caused by the action of an unaccustomed food.[14] They chose as an experimental organism the garden aphid (*Neomyzus circumflexus*), which is characterized by an ability to feed on various plants. The different food plants, however, are not equally beneficial to the aphids. Thus, in feeding on vetch, the aphids display a minimum mortality and maximum fertility. Peas are a less suitable food, and radish and mustard are the least beneficial. Feeding

[12] Armen Levonovich Takhtadzhan, "Priamoe prisposoblenie ili estestvennyi otbor? (O statisticheskikh zakonakh biologii)" ["Direct Adaptation or Natural Selection? (On the Statistical Laws of Biology)"], *Bot. zhurnal* [*Journal of Botany*], 1957, *42:* 607.

[13] A.F. Gubin and I.A. Khalifman, "Vliianie pishchi na porodnye priznaki medonosnoi pchely" ["The Effect of Food on Variety-Specific Traits in the Honeybee"], *Agrobiologiia* [*Agrobiology*], 1950, *no. 2:* 115-125.

[14] Eugenii Sergeevich Smirnov and E.S. Keleinikov, "Izmeneniia zhiznennosti i nasledovanie priobretennykh priznakov u Neomysus circumflexus" ["Changes in Viability and the Inheritance of Acquired Traits in Neomysus circumflezus"], *Zool. Zhurn.* [*Zoological Journal*], 1950, *29:* 52-68; Galina Valentinovna Samokhvalova, "Poluchenie napravlennykh nasledstvennykh izmenenii u tlei pri peremene kormovykh rastenii" ["Obtaining Directed Hereditary Changes in Aphids with a Change in Food Plants"], *Zool. Zhurn.* [*Zoological Journal*], 1954, *33:* 1032-1041; E.S. Smirnov and G.V. Samokhvalova, "Izmeneniia nasledstvennosti i zhiznennosti tlei pri smene kormovykh rastenii" ["Changes in Viability and Heredity in Aphids with a Change in Food Plants"], *Agrobiol.* [*Agrobiology*], 1955, *no. 2;* 61-77; E.S. Smirnov, "Teoreticheskoe obosnovanie nasleduemosti priobretennykh svoistv" ["Theoretical Basis for the Inheritance of Acquired Characters"], *Doklady na 7-m i 8-m ezhegodnykh chteniakh na pamiati N.A. Kholodkovskogo* [*Papers of the 7th and 8th Annual Readings in Memory of N.A. Kholodkovskii*] (Moscow-Leningrad: 1956), pp. 61-62; E.S. Smirnov, "Nasledovanie priobretaemykh svoistv v protsesse adaptatsii" ["The Inheritance of Acquirable Characters in the Process of Adaptation"], *Zhurn. obshchei biol.* [*Journal of General Biology*], 1957, *18:* 464-475; also in the collection *Nasledstvennost' i izmenchivost' rastenii, zhivotnykh i mikroorganizmov* [*Inheritance and Variability in Plants, Animals, and Microorganisms*], 1959, *1:* 743-753.

the aphids mustard leaves, the author discovered a rise in mortality and a decline in fertility which increased from generation to generation. In the seventh through the ninth generations, however, the mortality rate began to drop and fertility to increase. The authors regarded this result as an "hereditary habituation to a plant originally unsuitable for the cultivation of aphids." The habituation, according to them, "is realized according to the law of the inheritance of acquired characteristics" (1955, p. 70). A recently published book devoted to the problems of evolution appropriately brought this conclusion into question.[15] One of the authors, Abram L'vovich Zelikman, offered the following consideration. The ability of *Neomyzus* to feed on different plants depends on the genetic heterogenity of any given population of this aphid. This was noted, in particular, by Smirnov and Galina Valentinovna Samokhvalova, who confirmed that "individual variability both in fertility and in other indicators was quite sizeable."[15a] Quite a high mortality rate (80%) was displayed by aphids which had fed on mustard. Naturally the individuals with the greatest sensitivity to the unfavorable feeding conditions died, that is, a natural selection of the individuals most resistant to these conditions took place. A portion of these latter individuals undoubtedly had a hereditary resistance to the injurious effects of the unaccustomed food. This is testified to by the fact that the rise in fertility and the drop in mortality was first displayed only in the seventh through the ninth generations, when the favorable mutation (hereditary resistance to unaccustomed food) had accumulated through natural selection. Since Smirnov and his co-workers took into account the viability and fertility only of the whole experimental population and not of each individual line, the average drop in mortality and rise in fertility which they discovered must be attributed to the result of the elimination of those individuals less fertile and more sensitive to the injurious influence. In other words, this was a group form of natural selection. This conclusion would not hold true if it could be shown through accurate experiments that natural selection alone was not enough to achieve the given results, or if there were an assurance that natural selection of traits of viability and fertility did not occur in the experiments described. Smirnov and his co-workers, who attributed the inheritance of an acquired resistance to the influence of an unaccustomed food, themselves sensed the precariousness of their position, inasmuch as they all admitted that natural selection had played a certain role in their experiments.[15b]

[15] Zelman Isaakovich Berman, K.M. Zavadskii, A.L. Zelikman, A.A. Paramonov, and Iu. I. Polianskii, *Sovremennye problemy evoliutsionnoi teorii* [*Contemporary Problems of Evolutionary Theory*] (Moscow: 1967), pp. 332-333.

[15a] Smirnov and Samakhvalova (1955; n. 14), p. 64.

[15b] Smirnov (1956; n. 14).

At the "Lenin Hills" scientific-experimental station, beginning in 1952, high grade Jersey dairy bulls were bred with cows of various breeds. On the basis of the results, Trofim Denisovich Lysenko asserted that if half-breed bulls were abundantly fed on their mothers' milk and then mated with high-grade dairy cows, their offspring should be low in fertility and high-grade in milk production. He believed that such offspring would retain those characteristics in succeeding generations even in the absence of abundant feeding.[16]

An Academy of Sciences Commission investigated these assertions and came to the conclusion that "they are refuted by the factual data."[17] "In actuality," as the Academy of Sciences Presidium said in its corresponding resolution, "the fat content of hybrids in succeeding generations decreased."[18] "The use of pedigree bulls from 'Lenin Hills' is inadmissable for breeding purposes."[19]

This last example shows that a presumption of the inheritance of traits acquired during the individual life leads not only to false theoretical conclusions but also to an incorrect orientation in practical activities.

[16] "O rezul'tatakh proverki deiatel'nosti eksperimental'noi bazy i podsobnogo khoziaistva 'Gorki Leninskie' Akademii nauk SSSR" ["On the Results of an Investigation of the Activities of the Experimental Station and Subsidiary Agriculture of the 'Lenin Hills' Academy of Sciences of the USSR." In notes concerning the commission's paper, T.D. Lysenko stated, "This is a good example of the inheritance of acquired traits in animals," *Vestn. AN SSSR* [*Communications of the Academy of Sciences of the USSR*], 1965, *no. 11:* 62n.

[17] *Ibid.*, p. 21.

[18] *Ibid.*, p. 127.

[19] *Ibid.*, p. 128.

CHAPTER 16

Is the Inheritance of Immunity Possible?

Contemporary immunological literature does not discuss the question of the inheritance of immunity. It considers it impossible to transmit through the germ cells an acquired immunity to infectious and other types of diseases. Contemporary microbiologists and immunologists simply classify each immunity as inherent or acquired. Medical practice has required the repetition of protective vaccinations against smallpox, diptheria, etc. for every new generation, despite the immunization which many generations of forebears have undergone. The offspring are obviously born without inheriting the immunity acquired by their parents. In light of this experience, the chapter of Petr O. Sakharov's book entitled "The Inheritance of Acquired Immunity in Animals" has an anachronistic ring.[1] We need not discuss it in detail. In the 1880s and 1890s attempts were still being made to explain the presence of immunity in the offspring of immunized mothers and fathers. It had already been established by Paul Erlich that one must clearly differentiate phenomena of true inheritance of immunity from false inheritance, that is, the transmission of acquired immunity through the placental blood circulation or the mother's milk. The majority of workers in this field have denied the existence of phenomena of the former kind, that is, the transmission of acquired immunity via the hereditary apparatus of the germ cells. In those instances where the experiments seemed to speak of true inheritance of immunity, e.g., the experiments of V. Lambert on chicken paratyphoid and those of L. Webster on mouse typhoid, in fact selection had occurred. The individuals used for subsequent reproduction were those which had survived, that is, those which independent of the fact that their parents were immunized possessed a genotype giving immunity to the infection under study.

Unwarranted statements concerning the inheritance of acquired immunity to infectious diseases have appeared relatively recently.[2] The experiments of Sakharov and his associates give no basis for the assertion

[1] Petr O. Sakharov, *Nasledovanie priobretaemykh svoistv* [*The Inheritance of Acquirable Characters*] (Moscow: 1952).

[2] For example, in an article by the contemporary Lamarckist, E. Dechambre, "Reflexions sur les caractères acquis et sur leur transmissibilité," *Rev. gén. Sci. pures et appl.*, 1949, *56.*

that they prove the inheritance of acquired immunity.

In its day the series of works by M.F. Guyer and E.A. Smith created quite an impression. These experimenters introduced an emulsion of dissolved rabbit crystalline lens into chickens to obtain an anti-crystalline lens serum which was then injected into pregnant female rabbits. They calculated that this would act through the placenta upon the developing eyes and possibly the germ cells of fetuses. It must be noted first of all that no changes were displayed in the females which received the serum themselves. Of the rabbits born to them, a portion displayed various degrees of clouding of the crystalline lens and sometimes a decrease in eye size or impairment of the iris structure. Guyer and Smith asserted that the changes they had obtained were hereditary. Seven offspring were obtained from one experimental female rabbit, six normal and one male with impaired development of one eye. Among eighteen offspring produced by mating this male with a normal female, four females had eye defects. From two of these females, paired with normal males, nine offspring were obtained, five of which had impairments in eye structure.[3] Later these authors found eye defects in three out of six rabbits born to a female which had been injected with the anti-crystalline lens serum. One of the abnormal male offspring was crossed with a normal sibling, and they produced young with impairments in eye development.[4] Altogether in Guyer and Smith's experiments, six out of the twenty-one experimental females produced seventeen offspring (from a total of 161) with an impairment in eye structure, such as total lack of development, decrease in size, splitting of the iris, or cloudiness of the crystalline lens. The trait of defective eyes was inherited like a recessive trait, though the segregation of the trait was not exactly that which is characteristic of the inheritance of eye defects in general.

Discussing the results published by Guyer and Smith, Guyénot presented three possible explanations for the data obtained: 1. the expression of a recessive trait latent in the experimental females, 2. the appearance of a spontaneous mutation, or 3. the induction of a mutation by the injected serum. A mechanism that would account for the action of the anti-crystalline lens serum, particularly, for the induction of a specific mutation by an agent circulating in the blood, defies imaginations. The action of the anti-crystalline lens serum on parts of the eye other than the crystalline lens is also not understood.

Guyer and Smith's works were repeated and the results were not

[3] Michael Frederic Guyer and E.A. Smith, "Studies on Cytolysins. I. Some Prenatal Effects of Lens Antibodies," *J. Exper. Zool.*, 1918, *26:* 65–82; "II. Transmission of Induced Eye Defects," *ibid.*, 1920, *31: 171–223.*

[4] Michael Frederic Guyer and E.A. Smith, "Further Studies on Inheritance on Eye Defects Induced in Rabbits," *J. Exper. Zool.*, 1923–24, *38:* 449–475.

confirmed. Julian Sorell Huxley and A.M. Carr-Saunders obtained fifty-seven offspring from twelve female rabbits which had been injected with anti-crystalline lens serum. In a thorough ophthalmological examination of the offspring they discovered absolutely no eye defects.[5] G.F. Finlay injected pregnant mice with serum obtained from chickens or rabbits which earlier had been injected with a crystalline lens emulsion from a rat, bull, or ram. All eighty of the offspring had normal eyes. With active immunization, that is, by injecting pregnant rats and mice with a crystalline emulsion he also obtained normal offspring.[6]

As described in unpublished investigations, Guyénot, V. Bischler, and K. Ponse injected a crystalline lens emulsion taken from colts or young guinea pigs into guinea pigs that had been bred over several generations and consistently demonstrated an absence of hereditary eye anomalies.[7] The injections were administered repeatedly from the time of mating to the end of pregnancy. In a number of instances the males, too, were injected. In all, a hundred and fifty offspring without any sort of eye anomalies were obtained. In other experiments an optic nerve of the guinea pigs was severed or an eye was transplanted and in time resorbed. In both cases clouding of the crystalline lens occurred as a consequence of autoimmunization. No defects of the eye were displayed in the young which were born during the period of resorbtion and later. We may mention the even later work of Herman L. Ibsen and L.D. Bushnell, which also yielded negative results.[8]

Comparison of the experiments cited leads to the conclusion that we must doubt the very fact of a change in the eye of the young brought about by the injection into pregnant females of anti-crystalline lens serum. Guyer and Smith's data can likely be explained by the presence in their experimental setup of rabbits that possessed recessive genes for eye defects. A similar type of spontaneous mutation is quite often found in rodents.

[5] Julian Sorell Huxley and A.M. Carr-Saunders, "Absence of Prenatal Effects of Lens-antibodies in Rabbits," *Brit. J. Exper. Biol.*, 1924, *1:* 215–248.

[6] G.F. Finlay, "The Effect of Different Species' Lens Antisera on Pregnant Mice and Rats and Their Progeny," *Brit. J. Exper. Biol.*, 1924, *1:* 200–213.

[7] The results of these experiments are summarized in Guyénot's work *La variation et l'évolution* (Paris: 1930), vol. 1, p. 110.

[8] Herman L. Ibsen and L.D. Bushnell, "The Effects Produced on Parents and Descendants by the Injection of Calf Lens Material Directly into the Rabbit Parent," *Genetics*, 1934, *19:* 293–309.

CHAPTER 17

The Question of the Inheritance of Acquired Behavioral Traits

The idea of the inheritance of acquired habits was an integral component of Lamarck's evolutionary concept. Darwin repeatedly returned to the discussion of the possible transformation of acquired habits into the stable hereditary form of behavior called instinct. In the *Origin of Species* he examined three examples in particular detail: the instinct of the cuckoo to lay eggs in the nests of other birds, the slave-owning instinct of ants, and the hivebuilding instinct of honeybees. Discussing these passages, Aleksei Dmitrievich Nekrasov noted Darwin's confidence in the fact that many instincts could not be the result of the inheritance of acquired habits but are inherent forms of behavior. In particular, it was clear to Darwin that "habits of neuter social insects cannot be transmitted to their offspring."[1] Nekrasov cited the following passage from the *Origin,* "I am surprised that no one has advanced this demonstrative case of neuter insects against the well-known doctrine of Lamarck."[2] "Darwin himself," Nekrasov noted "did not use this example in order to refute the Lamarckian principle, he simply qualified it."[3] The degree of this qualification is clear from "A Posthumous Eassy on Instinct." which Darwin did not publish during his lifetime, but which appeared in George J. Romanes's book, *The Mental Evolution in Animals* (1883). The Russian translation of this essay is included in the third volume of Darwin's *Works*. "If we assume," wrote Darwin, "that a given habitual action will become hereditary, and it can be shown that this sometimes in fact happens, the similarity between that which was originally habit and that which was instinct becomes close."[4]

[1] Aleksei Dmitrievich Nekrasov, "Rabota Charlza Darvina nad 'Proiskhozhdeniem vodov' i rost eto evoliutsionnykh idei" ["Charles Darwin's Work on 'Origin of Species' and the Growth of his Evolutionary Ideas"], *Soch.* [*Works*], 1939, *3:* 65. [This particular passage cannot be identified in the original, but see *Origin* (1859), p. 237.]

[2] Charles Darwin, *Proiskhozhdenie vodov* [*The Origin of Species*], in *Soch.* [*Works*], vol. 3, p. 483. [*Origin* (1859), p. 242.]

[3] Nekrasov (n. 1), p. 65.

[4] Darwin (n. 2), p. 723. [This passage cannot be identified in the original but see Charles Darwin, "A Posthumous Essay on Instinct" in George John Romanes, *Mental Evolution in Animals* (London: Kegan Paul, Trench, & Co., 1883), particularly pp. 383-384.]

In *The Origin of Species* and *The Expression of Emotions in Man and Animals,* Darwin showed much less caution in his consideration of the possibility of the inheritance of habits. Among a host of analogous passages, we may cite the following for illustration. "Certain acts of reason—when, for example, birds on oceanic islands learn to avoid man—after being repeated by several generations, are finally transformed into instincts and transmitted by heredity."[5] Or "One can scarcely doubt that some sort of physical changes take place in nerve cells or nerves which must function frequently; otherwise it would be impossible to understand how the tendency toward certain acquired movements is transmitted."[6] In support of this idea Darwin cited the special gaits which have been developed in certain breeds of horses, the ability of hunting dogs to point, and other examples. It is not clear why Darwin did not even attempt to draw upon the principle of artificial selection to explain the appearance and fixation of these characteristics of behavior.

Commentators on the fifth volume of Darwin's *Works* unjustifiably wrote that Darwin's position on the inheritance of acquired characteristics "was expressed in exhaustive clarity and fullness." From the data in chapter fourteen and from the references just made, it is evident that Darwin was far from being certain of the inheritance of acquired characteristics in general and the inheritance of habits in particular. Moreover, the commentators' assertion that the hypothesis of the inheritance of acquired habits agrees with contemporary physiology was completely unfounded.[7]

Advocates of the inheritance of acquired behavioral traits also referred to Engels as though he accepted such inheritance without question, particularly as applied to man's laboring activities. The following passage is quoted with particular frequency: "Only due to work, due to adaptation to all new operations, due to the inheritance of muscle, ligament, and over a longer period of time, of bone development, and due to the constant application of these new improvements to new and increasingly more complex operations, only due to all these did the human hand reach that degree of perfection at which it could, as if by magic, bring to life the paintings of Raphael, the statues of Thorvaldsen, the music of Paganini."[8] It

[5] Charles Darwin, *Proiskhozhdenie cheloveka i polovoi otbor* [*The Descent of Man and Sexual Selection*], in *Soch.* [*Works*], 1953, *5:* 188. [This passage could not be located in the original; see however, *The Descent of Man,* (2nd ed.; New York: D. Appleton & Co., 1897), p. 80.]

[6] Charles Darwin, *Vyrazhenie emotsii u cheloveka i zhivotnykh* [*The Expression of Emotions in Man and Animals*], in *Soch.* [*Works*], 1953, *5:* 709. [This passage could not be located in the English original.]

[7] Commentary in the book *Vyrazhenie emotsii u cheloveka i zhivotnykh* [*The Expression of Emotions in Man and Animals*], in *Soch.* [*Works*], vol. 5 (1953), p. 1008.

[8] Friedrich Engels, "Rol' truda v protsesse prevrashcheniia obez'iany v cheloveka"

(*contd.*)

does not at all follow from this quotation that Engels had in mind the inheritance of the results of various habituated motor reactions. His words may be interpreted in a Darwinian as well as a Lamarckian sense. They may assert that hereditary changes which arise in muscles, ligaments, and bones and which are useful for work and which consequently come under the influence of natural selection are perfected through exercise in those individuals who already [innately] possess them.

It was often noted during the discussions on methodological issues in biology which took place in the Soviet Union during the 1920s and 30s that "on the question of the descent of man and the role of labor in this process Engels had in mind not so much the biological problem as the socio-historical one."[9] At the same time, one can find in Engels an explicit statement concerning the inheritance of acquired traits, an opinion shared during this time by practically all biologists, doctors, and practically oriented agriculturalists. A.L. Takhtadzhan, in a critical survey devoted to the question of the inheritance of acquired traits, correctly noted with respects to Engels's view on this matter, "Reading these lines one must bear in mind that they were written at a time when Francis Galton and August Weismann were supporters of the inheritance of acquired characters."[10]

When physiologists deal with material which directly relates to their field of research, they always document their assertions and even their hypotheses with references to experimental data and take care that their arguments are logically set forth. In describing the methodology of their experiments, they insure the reliability of the results with an appropriate control and check the reproducibility of the experimental data obtained. Nevertheless, when addressing a question concerning another branch of the biological sciences, for example, the questions of variability and heredity, which also can only be solved experimentally, the same physiologists often forget the rigorous requirements which equally pertain to the execution of these empirical investigations.

Thus, certain physiologists, without recourse to specific research, have suggested that forms of behavior acquired during the course of an individual life may be transmitted to the offspring. For example, Vladimir Mikhailovich Bekhterev wrote, "With the constant repetition of one and

["The Role of Work in the Process of Transformation from Ape to Man"], in Karl Marx and Friedrich Engels, *Soch.* [*Works*], 1961, *20:* 488.

[9] Boris Petrovich Tokon. Paper given at the general meeting of biologist materialists of the Communist Academy, in the collection, *Protiv mekhanisticheskogo materializma* [*Against Mechanistic Materialism*] (Moscow-Leningrad, 1931). M.L. Levin and B.M. Zavadovskii expressed the same idea at this meeting.

[10] Armen Levonovich Takhtadzhian, "Priamoe prisposoblenie ili estestvennyi otbor?" "Direct Adaptation or Natural Selection?", *Bot. zhurn.* [*Journal of Botany*], 1957, *42:* 607.

the same adaptive act, distinctive habitual movements are acquired that through the extended exercise of very special mechanisms are formed out of certain well-worn pathways in the nervous system. As a consequence, the transfer to and fixation of such acts in offspring may occur by means of the inheritance of prepared (already established) nerve mechanisms which significantly simplify the elaboration and acquisition of similar pathways in a series of succeeding generations."[11]

The unsubstantiated nature of such claims concerning the inheritance of "special mechanisms" and "well-worn pathways" created in the nervous system by exercise was not obvious to everyone. It must be noted, however, that Ivan Mikhaylovich Sechenov approached this question with a completely different attitude. "The ability . . . to adapt behavioral actions to altered conditions," he wrote, "is gained only through the individual life experience and is considered nonheritable."[12]

Ivan Petrovich Pavlov was one of the few physiologists who made an attempt to determine experimentally the possibility of the inheritance of acquired behavioral traits. We must describe in some detail the events connected with the study of this question in Pavlov's laboratory.[13]

In his earliest studies of the higher nervous functions, Pavlov did not take up the genetic side of the question and expressed personal opinions on this subject only hypothetically and in passing. Speaking at the Ninth International Congress of Physiologists in Gröningen in 1913, Pavlov noted, without recourse to any experimental evidence, "It may be admitted that certain newly-formed conditioned reflexes are later transformed into unconditioned ones by heredity."[14] In a paper prepared for the International Congress of Psychiatrists, Psychologists, and Neurologists held in Switzerland in 1914, Pavlov once more unambiguously stated, without corroborating his ideas with concrete data, "It is highly probable (and we already have factual data which suggest this) that newly arising reflexes

[11] Vladimir Mikhailovich Bekhterev, *Psikhika i zhizn'* [*Psychology and Life*], (2nd ed.; St. Petersburg), p. 3.

[12] Ivan Mikhaylovich Sechenov. *Fiziologicheskie ocherki* [*Studies in Physiology*] (St. Petersburg: 1884), p. 164.

[13] They are elucidated in the following articles: Gregory Razran, "Pavlov and Lamarck. The great Russian Scientist once reported experiments in support of Lamarck. Were his final views Lamarckian?" *Science*, 1958, *128:* 758-760; Conway Zirkle, "Pavlov's Beliefs," *Science*, 1958, *128:* 1476; Razran. "Pavlov, the Empiricist," *Science*, 1959, *130:* 916; Vitezslav Orel and J. Jindra, "I.P. Pawlows Stellung zu Gregor Mendel und zur Genetik," *Biol. Rundschau*, 1967, *5:* 71-75.

[14] Ivan Petrovich Pavlov, "Dvadtsatiletnii opyt ob'ektivnogo izucheniia vysshei nervnoi deiatel'nosti zhivotnykh. XXII. Issledovanie vysshei nervnoi deiatel'nosti" ["Twenty year Experiment in the Objective Study of the Higher Neural Activity of Animals. XXII. Research in Higher Neural Activity"], rept. in *Polnoe sobr. soch.* [*Complete Collected Works*], 1951, *3:* 273.

are continuously changing to permanent ones, provided that identical conditions are maintained in a series of succeeding generations."[15]

Pavlov first reported his attempts to confirm experimentally his hypothesis of the inheritance of acquired (conditioned) reflexes in four presentations made during the summer of 1923 in America and England.[16] "The most recent (and still unfinished) experiments," said Pavlov, "show that conditioned reflexes (i.e., higher nervous functions) are heritable. At the present time several experiments on white mice have been completed. The animals were conditioned to an electric bell; they had to run to the feeding place at the bell's sound. The following results were obtained. The first generation of white mice required three hundred trials, coupling the sound of the bell with the presentation of food, to train them to run to the feeding place when the bell rang. The second generation required only a hundred trials to achieve the same result. The third generation learned this after only thirty-nine trials. The last generation which I saw before leaving Petrograd learned this lesson after five repetitions.... I think it very probable that after some time a new generation of mice will run to the feeding place on hearing the bell, with *no* previous lesson."[17] In the cited report, Pavlov relied on experimental data of his co-worker, N.P. Studentsov, published in the following year.[18]

In an article in memory of Pavlov, published in *Biologicheskii Zhurnal* (1936, 5: 387-402) and reprinted in an abridged version in 1967, Nikolai K. Kol'tsov discussed the Studentsov experiments and noted, "Ivan Petrovich [Pavlov] allowed himself to be convinced that the inheritance of acquired characteristics—conditioned reflexes—had occurred."[19]

[15] *Ibid.*, p. 281.

[16] At the end of July 1923 at the Marine Biological Laboratories at Woods Hole, on July 5 at Chicago University, on July 7 at the sanatorium at Battle Creek, and then at the XI International Congress of Physiologists in Edinburgh. The Chicago lecture ["The Identity of Inhibition with Sleep and Hypnosis"] was published in *Scientific Monthly*, 1923, *17:* 603-608, and one identical to it in the *Transactions of the Edinburgh Congress* (*Quarterly Journal of Experimental Physiology*), 1923, Suppl. vol.: 39-43. The shorter lecture at Battle Creek appeared in the Bulletin of the *Battle Creek Sanatorium*, 1923, *19:* 1-4 and in *Science*, 1923, *58:* 359-361. The text of the *Science* article appears under the title "Novyi issledovaniia po uslovnym refleksam" ["New Research on Conditioned Reflexes"] in *Poln. sobr. soch.* [*Complete Collected Works*], 1951. *3*, Bk. 2: 431-432.

[17] Paul Kammerer [paraphrases this passage and quotes the last sentence] in his book, *Neuvererbung oder Vererbung erworbener Eigenschaften* (Stuttgart-Heilbronn: 1925) [see, Kammerer, *The Inheritance of Acquired Characteristics*, trans. A. Paul Maerker-Brandon (New York:Boni and Liveright, 1924), pp. 186-187.]

[18] N.P. Studentsov, "Nasledovanie priruchennosti u belykh myshei" ["The Inheritance of Tameness in White Mice"], *Russkii fiziol. zhurn.* [*Russian Journal of Physiology*], 1924, *7:* 312.

[19] Nikolai Konstantinovich Kol'tsov, "Trud zhizni velikogo biologa" ["The Life of a Great Biologist"], in the collection *I.P. Pavlov v vospominaniiakh sovremennikov* [*I.P. Pavlov in the Recollections of his Contemporaries*] (Leningrad: 1967), p. 112.

During the First Congress of Zoologists, Anatomists, and Histologists in Petrograd in 1923, Kol'tsov visited Pavlov specifically to persuade him of the impossibility of the inheritance of acquired reflexes by reviewing the still unpublished works of Studentsov. "It was not the mice who learned, but the experimenters, who up until that time had had no experience in training mice." After this discussion Kol'tsov had the impression that Pavlov agreed with his conclusions. Pavlov still found it possible, however, to relate Studentsov's experiments in the presentations mentioned above. But the conversations with Kol'tsov as well as comments in the press had their effect, and upon meeting Kol'tsov in 1925, Pavlov told him, "Now I work only with dogs, which I know. I no longer wish to work with mice." "Nonetheless," continued Kol'tsov, "he showed me mice with which his co-worker, E.A. Ganike, continued to work. This, it seems, was already the eighth generation of trained mice.... The mice quickly, after only five to seven trials, learned to come to the bell. And I asked, 'But did you try to test mice whose parents had not been trained?' The answer was decisive. 'Yes, we tried. We even obtained them from another city to eliminate all doubt. In this apparatus they also learn after five to seven trials.' Any misunderstanding had been completely clarified."[20]

Leonid Georgievich Voronin reported the same thing concerning a further check of Studentsov's experiments. "The test was carried out in an experimental installation specially constructed by Ganike, where the experiments took place without the direct participation of the experimenter. Ganike studied more than twenty-five generations of mice and found no sign of the inheritance of conditioned reflexes. The experiments were not concluded until after I.P. Pavlov's death, but the results remained unpublished.... Thus the myth created by the supporters of the view that conditioned reflexes are inherited should be dismissed and considered an annoying misunderstanding."[21]

Following Pavlov's 1923 papers, attempts to verify the results were undertaken and published in various laboratories. Edwin Carleton MacDowell reported experiments on rats in a circular maze. The differences in average maze-running performance were not statistically significant for the three groups of rats—those whose parents had not been trained and the two generations of offspring of trained rats. MacDowell reviewed analogous experiments on mice in a simple maze by H.J. Bagg and the results of his own experiments just mentioned. He concluded that "the training of the ancestors did not facilitate the learning of the descendants."[22] The

[20] *Ibid.*, p. 113.

[21] Leonid Georgievich Voronin. *Lektsii po sravnitel'noi fiziologii nervnoi sistemy* [*Lectures on the Comparative Physiology of the Nervous System*] (Moscow: Moscow State University, 1957), p. 169.

[22] Edwin Carleton MacDowell. "Experiments with Rats on the Inheritance of Training," *Science*, 1924, *59:* 302-303.

work of E.M. Vicari was published next to MacDowell's article. While training mice in a simple maze, she also found no decrease in the time for passage through the maze in three successive generations. Like MacDowell, she concluded that "the later generations have not been aided in learning the maze by the training of the ancestors."[23] In the same year Thomas Hunt Morgan published an article in the *Yale Review,* soon afterwards translated into Russian, in which he presented the experiments reported by Pavlov and other examples of false evidence of the inheritance of acquired traits, and then presented contradicting experiments by Bagg, MacDowell, and Vicari. Summarizing the views on this subject, he remarked, "how simple would our educational questions become if our children at the sound of the school bell learned their lessons in half the time their parents required! We might soon look forward to the day when the ringing of bells would endow our great-grandchildren with all the experience of the generations that had preceded them."[24] Pavlov's data and the results of MacDowell's and Vicari's works were also compared in Wilhelm Johannsen's genetics text.[25]

Under Kol'tsov's direction, Maria P. Sadovnikova-Kol'tsova carried out experiments designed to test for the inheritance of learning. According to her data the index (the log of the number of minutes needed to pass through the maze) for rats descended from untrained parents was, on the average, 1.85 ± 0.13. The index for rats which were the offspring of trained parents was $0.96 \pm .04$. The difference was 0.11 ± 0.14. From this she concluded that the "the teaching of parents does not influence the abilities of the offspring."[26]

In the following years the American psychologist William McDougall reported on experiments on the training of rats.[27] McDougall presented his initial theoretical stance in the following words: "If the Lamarckian hypothesis be valid, if it be true that modifications of function and structure, acquired by the individual organism in consequence of its efforts to adapt itself to its environment, may be in some degree, however slight, transmitted to its descendants, then we have in outline an adequate theory of

[23] E.M. Vicari, "The Non-Inheritance of the Effects of Training," *Science,* 1924, *59:* 303.

[24] Thomas Hunt Morgan, *Nasledstvenny li priobretennyi priznaki?* [*Are Acquired Traits Inherited?*] (Leningrad: 1925), pp. 9–10. [In the original this appears as an article with the same title in *Yale Review,* 1923–24, *13:* 712–729.]

[25] Wilhelm Johannsen, *Elemente der exakten Erblichkeitslehre* (Jena: 1926).

[26] Maria P. Sadovnikova-Koltzova, "Genetic Analysis of Temperament of Rats," *J.Exper. Zool.,* 1926, *45:* 301–318. [Quotation appears on p. 318.]

[27] William McDougall, "An Experiment of the Testing of the Hypothesis of Lamarck," *Brit. J. Psychol.,* 1926–27, *17:* 267–304; W. McDougall, "Second Report on a Lamarckian Experiment," *ibid.,* 1930, *20:* 201–218; J.B. Rhine and W. McDougall, "Third Report on a Lamarckian Experiment," *ibid.*. 1933–34, *24:* 213–235.

organic evolution; and, further, we are able to assign to mind, or, in other words, to purposive, teleological, or hormic[28] activity, an intelligible and leading role in the drama. On the other hand, if we can find no warrant for accepting the Lamarckian hypothesis, then we remain utterly in the dark as to the nature of the evolutionary process; . . . natural selection . . . does not give us a tenable theory of evolution, so long as we postulate only fluctuating variations or indeterminate mutations."[29]

It was with this kind of idealistic, teleological pre-conception that McDougall approached his research. In his experiments rats were trained to avoid an electric shock at a lighted exit and to choose the darkened exit where there was no shock. According to McDougall's data, the average number of mistaken choices for more than thirty generations of trained rats was significantly less than for the control rats. These results were critically discussed by Tracy M. Sonneborn, F.A.E. Crew, Morgan, and W.E. Agar. Sonneborn felt that McDougall's experiments had included an unconscious selection of rats of a genetically conditioned behaviour type which made their training easier.[30] He further pointed out the importance of differences in the strength of the electric shock. Given a current of greater strength, rats learn to find the right exit faster. It was significant that McDougall had applied stronger electric stimuli in the later experiments. Crew analyzed McDougall's data in detail and came to the conclusion that the variety of factors capable of effecting the results of such an experiment was so large that it was impossible to draw any kind of well-founded conclusions about the results obtained.[31] Particularly essential, according to Crew, was the fact that a very significant and obviously hereditarily conditioned variation in behaviour was observed in the initial control. Morgan also directed attention to the wide range of variation in the experiment and the control which hindered evaluation of McDougall's results.[32] According to the testimony of V. Borovskii, who in 1929 attended the Eighteenth International Congress of Physiologists in Boston, the reading of McDougall's paper at that time drew quite sceptical remarks.[33]

[28] From the Greek ὁρμή —onset.

[29] McDougall (n. 27), 1926–27, *17:* 268.

[30] Tracy Morton Sonneborn, "McDougall's Lamarckian Experiment," *American Naturalist,* 1931, *65:* 541–550.

[31] Francis Albert Eley Crew, "Inheritance of Educability. A First Report on an Attempt to Examine Professor McDougall's Conclusions Relating to his Experiment for the Testing of the Hypothesis of Lamarck," *Proc. 6th Internat. Congr. Genetics,* 1932, *1:* 121–134.

[32] Thomas Hunt Morgan, *Eksperimental'nye osnovy evoliutsii* [*The Experimental Basis of Evolution*], trans. G.D. and G.S. Karpechenko (Moscow-Leningrad: 1936), pp. 165–166, 220–222. [This undoubtedly refers to Morgan's *The Scientific Basis of Evolution* (New York: W.W. Norton & Co., 1932).]

[33] V. Borovskii, "Vystuplenie na obshchem sobranii obshchestva biologov-materialistov" ["Presentation at the General Meeting of the Society for Biologist-Materialists"], in the

(*contd.*)

Later Agar attempted to verify these experiments. He continued for more than twenty years, during which time he studied more than one hundred generations of rats (over 4,500 individuals). In 1931 he had already come to the conclusion that the results of training were not inherited.[34] Further experiments fully confirmed this. The concluding report of Agar and his co-workers was published in 1954.[35] Following these studies there was no longer any basis for citing McDougall's data as evidence of the inheritance of acquired behavioral features. Nonetheless, Philip G. Fothergill, an English botanist and historian of evolution theory with Lamarckian leanings, wrote about McDougall's experiments and clearly overestimated their persuasivenss and significance. He said they were, "models of their kind and must rank among the classics of scientific literature."[36] Having presented McDougall's data in detail, including the reproduction of numerical tables, Fothergill mentioned only Crew's contrary experiments and considerations, and he arbitrarily considered them unconvincing. He completely omitted data of McDougall's other critics, including Agar, who had demonstrated the noninheritance of acquired forms of behaviour.

Following this digression it is appropriate to return to Pavlov's evolutionary views on the question of the inheritance of conditioned reflexes and to the portrayal of his views in the literature.

In 1927 Gleb Vasil'evich Anrep's English translation of Pavlov's book, *Conditioned Reflexes* (London: Oxford University Press, 1927) appeared. (In Russian the book is entitled *Lecture on the Work of the Large Hemispheres of the Brain.*) Pavlov wrote a special preface to it and made annotations. In particular, he added the following footnote on page 385: "Experiments which were briefly reported at the Edinburgh International Congress of Physiologists (1923) concerning the inherited ease of establishing certain conditioned reflexes in mice, turned out to be very complex, unreliable, and above all, extremely difficult to control. They are now being subjected to further investigation under more rigorous conditions. At present the question of inheritance of conditioned reflexes must be considered completely open."

In 1927 E.S. Smirnov published a pamphlet, "The Problem of the Inheritance of Acquired Characters." The author cited Studentsov's

collection *Protiv mekhanisticheskogo materializma* [*Against Mechanistic Materialism*] (Moscow-Leningrad: 1931), p. 63.

[34] Wilfred Eade Agar, "A Lamarckian Experiment Involving a Hundred Generations with Negative Results," *J. Exper. Biol.*, 1931, *8:* 95-107.

[35] Wilfred Eade Agar, F.W. Drummond, O.W. Tiegs, and M.M. Gunson, "Fourth (Final) Report on the Test of McDougall's Lamarckian Experiment on the Training of Rats." *J. Exper. Biol.*, 1954, *31:* 307-321.

[36] Philip G. Fothergill, *Historical Aspects of Organic Evolution* (London: 1952), p. 262. [Quotation follows English original.]

experiments and Pavlov's original positive evaluation of them. Max L. Levin printed a review of this pamphlet in *Pravda* (no. 106, 13 May 1927) in which he reproduced the text of Pavlov's letter of 1 March 1927 answering an inquiry by V.K. Hutton. Pavlov had written, "The original experiments on the inheritance of conditioned reflexes in white mice have up to this time never been verified with improved methodology and more rigorous controls. Therefore I must not be counted among those authors who support such inheritance."[37]

According to Grunberg's testimony at the Eighteenth International Congress of Physiologists in Boston in 1929, Pavlov confirmed that the repetition of experiments on which he had reported in 1923 showed that the earlier results, that is, the more rapid establishment of conditioned reflexes in mice that had descended from trained parents, depended on an increase in the experimenter's experience.

In a monograph devoted to the history of Russian physiology, Khachatur Sergeevich Koshtoiants reviewed Studentsov's experiments and then pointed out that Pavlov was compelled to agree with the objections to these experiments advanced by geneticists, in particular by Morgan.[38] Pavlov did not include the text of the 1923 lectures in any of the editions of *A Twenty-year Experiment in the Study of the Higher Nervous System* although he updated them with earlier unpublished papers and articles on the problem of conditioned reflexes. The question of the inheritance of conditioned reflexes is also essentially unmentioned in the five volumes of *Pavlovian Environments,* which includes everything that Pavlov presented during laboratory colloquia of the 1930s.

Pavlov had presented his earlier positive results in a 1923 article in *Science* (see fn. 16). The Russian translation of that article first appeared only in 1949 in the fifth volume of the *Collected Works* and then in 1951 in the second book, volume III, of the second edition of Pavlov's works.

In 1949 Petr Stepanovich Kupalov published Pavlov's 1912/1913 "Lectures on Physiology" that he had taken down in shorthand. Pavlov did not look over the transcription of the notes, which undoubtedly explains why the following passage remained in the text of the ninth lecture: "Are conditioned reflexes transmitted by heredity? There is no rigorous proof of it, science has not yet reached that point. But one must believe that, given

[37] Regarding the doubt expressed in the literature concerning the authenticity of Pavlov's letter, Voronin wrote, "There is no reason to doubt that these words were Pavlov's own. There was hardly anyone during Pavlov's lifetime who would have dared to attribute to him another's words with such a weighty content." Leonid Georgievich Voronin, *Kurs lektsii po fiziologii vysshei nervnoi deiatel'nosti* [*A Course of Lectures on the Physiology of Higher Nervous Activity*] (Moscow: 1965), p. 68.

[38] Khachatur Sergeevich Koshtoiants, *Ocherki po istorii fiziologii v Rossii* [*Studies in the History of Physiology in Russia*] (Moscow-Leningrad: 1946), p. 292.

a prolonged period of development, firmly established reflexes may become inherent.''[39]

Certain of Pavlov's biographers assiduously propagandized views which he himself had rejected. Thus, Iurii Petrovich Frolov asserted that Pavlov ''recognized and proved the inheritance of physiological traits and features (reflexes) acquired by the organism in the course of its individual life.''[40]

Kirill Mikhailovich Bykov wrote on this subject in the same vein. ''Pavlov's study of the evolutionary traits of the nervous system, in which the problem of the fixation in heredity of certain acquired reflexes was crucial, takes on a special significance for biology.'' Bykov called ''crucial'' that which was an insignificant episode in Pavlov's vast scientific career and which, in fact, turned out to be the experimental error of a colleague to whom Pavlov had entrusted the execution of the investigations. To lend persuasiveness to his assertions, Bykov cited the passage quoted above (fn. 15) where Pavlov merely suggested the possibility of inheritance of acquired reflexes. Bykov wrote further that he had at his disposal ''new and diverse facts once again confirming Pavlov's predictions concerning the flexibility of neural processes as revealed through the study of conditioned reflexes. These processes, when systematically subjected to alterations, are fixed in some cases within a definite number of generations and in other cases over a long series of generations.''[41] It is strange that such a crucial assertion was not accompanied by a reference to the published experiments or by information on the nature, methodology, and concrete results of the experiments. One is forced to believe that in this instance, as has often happened with assertions concerning the inheritance of acquired characteristics, the ''hoped for and expected'' was passed off as the ''actual.'' There is no need to speak of the damage which such unfounded assertions have done. On occasion they have been cited by other authors as reliable data. For example, in P.O. Sakharov's book, along with a number of other unfounded assertions concerning the inheritance of acquired traits, the following is found: ''Investigations conducted . . . under the direction of K.M. Bykov, have proved conclusively the inheritance of newly acquired reflexes.''[42,43]

[39] Ivan Petrovich Pavlov, *Polnoe Sobranie Sochinenii* [Complete *Collected Works*] (2nd ed.; 1952), *5:* 95.

[40] Iurii Petrovich Frolov, *I.P. Pavlov—velikii russkii uchenyi* [*I.P. Pavlov—Great Russian Scientist*], (2nd ed. rev.; Moscow: 1952), p. 114.

[41] Kirill Mikhailovich Bykov, ''Uchenie I.P. Pavlova i sovremennoe estestvoznanie'' [''The Studies of I.P. Pavlov and Contemporary Natural Science''], *Izbr. proizv.* [*Selected Works*], vol. I (Moscow: 1953), p. 391.

[42] Petr O. Sakharov, *Nasledovanie priobretennykh svoistv* [*The Inheritance of Acquired Characters*] (Moscow: 1952), p. 237.

[43] E.S. Smirnov expressed similar views.

Unproven assertions concerning the inheritance of acquired forms of behavior are also found in a book by D.A. Biriukov. It contains a reference to the work of Viktor Konstantinovich Fedorov, who studied the hereditary fixation of the results of training and, according to Biriukov, ''obtained quite convincing results.''[44] By Fedorov's own account, he found that the rate of alteration of conditioned reflexes in the offspring of trained parents was greater than in offspring born to the same parents before training occurred. The former rate, however, was characterized by great individual variation. Moreover, as Fedorov wrote, ''There is one objection which we remain unable to counter: the possibility that in the control group of mice there is an accidental selection in the direction of a decrease in the plasticity of the neural processes.''[45] The author did not bother to ask here what was the nature of the neural mechanisms responsible for the transfer of the results of training through the sex cells of trained animals to their offspring. Moreover, he treated the issue as if the inheritance of altered reflexes were irrefutably proven.

Fedorov's position on the possibility of the inheritance of conditioned reflexes changed over the years. He began his early work on this subject assuming the existence of ''incontestable data pointing to external factors that cause changes in the parent individuals and, in the same way, under certain conditions, cause changes in the offspring.''[46] In the 1956 work mentioned, data were introduced that the author accepted, albeit with reservations, as evidence of the inheritance of acquired behavioral features. In a later survey article devoted to the question of the inheritance of forms of behavior, however, Fedorov did not even refer to his own experiments in which he had attempted to demonstrate the inheritance of conditioned reflexes.[47]

Biriukov's book cited above also discusses experiments by A.B. Kogan, who trained water fleas (*Daphnia*) to feed in the dark.. In the first six

[44] D.A. Biriukov, *Ekologicheskaia fiziologiia nervnoi deiatel'nosti* [*Ecological Physiology of Neural Activity*] (Moscow:1960) p. 49.

[45] Viktor Konstantinovich Fedorov, ''Vliianie trenirovki nervnoi sistemy myshei na vysshuiu nervnuiu deiatel'nost' potomkov chetvertogo pokoleniia'' [''The Influence of Training the Nervous System of Mice on the Higher Neural Functions of Offspring of the Fourth Generation''], *Tr. In-ta fiziol. im. Pavlova* [*Transactions of the Pavlov Institute of Physiology*], 1956: *5*, 143.

[46] Viktor Konstantinovich Fedorov, ''Vliianie trenirovki nervnoi sistemy roditelei na podvizhnost' nervnykh protsessov potomkov (u myshei)'' [''The Influence of Training the Nervous System of Parents on the Mobility of Neural Processes in Offspring (in Mice)''], *Tr. In-ta fiziol. im Pavlova* [*Transactions of the Pavlov Institute of Physiology*], 1953, *2:* 276-286.

[47] Viktor Konstantinovich Fedorov, ''Sovremennoe sostoianie genetiki povedeniia'' [''The Present State of Behavioral Genetics''], *Zhurn. Byssh. nervn. deiat.* [*J. of Higher Nervous Function*], 1966, *16:* 38-51.

generations there were no individual which displayed negative phototaxis. In the seventh and eighth generations the number of such individuals increased. In the ninth and tenth generations the numbers again dropped, they reached zero in the eleventh and twelfth generations, and then increased once more. From these experiments Kogan concluded that "the conditioned reflex that had been fixed over the course of several generations, became inherently unconditioned." [48]

The same author introduced these data in a textbook, where he appended to them the more cautious conclusions that "in order to judge the genetic significance of the observations, further work including various controls is necessary." [49] Judging by the lack of subsequent publications, these experiments must not have been carried out.

Following references to Fedorov's and Kogan's work, Biriukov in his book asserted that without fixation of these links in phylogenesis, that is, without the inheritance of acquired characteristics, Pavlov's studies on the adaptive significance of conditioned reflexes lost their meaning.

The adaptive function of conditional reflexes in the individual life is indisputable, and no one contests Pavlov's studies concerning their adaptive significance, whether or not such reflexes are inherited. Their inheritability should not be postulated, but tested with the same rigor as all similar experimental investigations of higher neural functions. Proof of the inheritance of acquired behavioral traits which satisfies this requirement is lacking. On the contrary, there are data that invite an explanation of the evolution of biologically useful forms of behavior without the assumption of the inheritance of acquired reactions to external influences.

Conwy Lloyd Morgan, at the end of the last century, accepted the theoretical possibility that individual, nonheritable acquired traits of behavior might be replaced by hereditary ones. "In addition to a particular heritable structure or mode of reaction, the organism inherits a certain amount of natural plasticity. . . . The specimens whose natural plasticity corresponds to the given conditions change and survive. . . . Such modification occurs from generation to generation, but, being only a modification, it is not inherited. The results of the modification are not transmitted to the hereditary substance. But variations [i.e. hereditary alterations—L.B.] which occur in the same direction as the modification . . . may develop unhindered. . . . Any hereditary variation similar in direction to these modifications strives to support them. . . . A hereditary disposition to a certain modification arises in a similar manner. The longer the process continues

[48] A.B. Kogan and A.N. Semenovykh, "O nasledstvennom zakreplenii uslovnykh refleksov" ["On the Hereditary Fixation of Conditioned Reflexes"], *Priroda* [*Nature*], 1955, *no. 9*:110-111.

[49] A.B. Kogan, *Osnovy fiziologii vysshei nervnoi deiatel'nosti* [*Fundamentals of Higher Nervous System Physiology*] (Moscow: 1959), pp. 255-256.

. . . the more likely the accumulation of hereditary variations that in all ways correspond to . . . the plastic modification." [50]

In a work devoted to the inheritance of behavioral traits in dogs, Leonid Viktorovich Krushinskii referred to these ideas of Morgan and compared them with the contemporary understanding of the role of nonheritable variation in evolution (I.I. Schmalhausen, E.I. Lukin, V.S. Kirpichnikov). "Given the emergence in a population of some individually acquired, biologically useful form of behavior," wrote Krushinskii, "conditions for the action of natural selection may be created which favor the substitution of "external" for "internal" factors for determining the emergence of this behavior. The process of such a replacement can be understood as the fixation in a population of an inherent, instinctive behavior which develops through selection of [genetic] material that has its realization in individually acquired behavior of the animal." [51] Proceeding from the stated ideas as applied to the evolution of forms of behavior, Krushinskii came to the conclusion that "the basic guiding force developing inherent, unconditioned reflex behavior out of individually acquired behavior must be the natural (or artificial) selection of hereditary tendencies which in turn give rise to this or that individually acquired behavioral reaction." [52]

Despite the factually well-founded conviction that acquired behavioral traits were not inherited and could only be detected in the evolutionary process in the form of inherent tendencies, claims concerning the inheritance of acquired reflexes continued to appear in print. Among such claims were Kogan's conclusions about his experiments with Daphnia. Krushinskii evaluated these experiments in a short but cogent article in which he dealt with the whole problem of the inheritance of behavior. In Kogan's studies of the group behavior of Daphnia, as Krushinskii correctly noted, individual survival rates were not taken into consideration, nor were individual reproduction rates as dependent on the rate of establishing the conditioned reflex of preferring a dark habitat, that is, as dependent on the very condition which favored selection. The maintenance of a nonheritable adaptation to the action of an external factor may lead to the substitution of that adaptation by an externally similar hereditary trait. "The restructuring of the genotype of a population through natural selection against a

[50] Conwy Lloyd Morgan, *Privychka i instinkt* [*Habit and Instinct*], trans. M. Cheninskaia (St. Petersburg: 1899), pp. 289-290. [The English original of this work appeared in 1896. These excertps could not be precisely identified, but see chapter 13, "Are Acquired Habits Inherited?," and chapter 14, "Modification and Variation," for rough equivalents.]

[51] Leonid Viktorovich Kruchinskii, "Nasledstvennoe 'fiksirovanie' individual'no priobretennogo povedeniia zhivotnykh i proiskhozhdenie instinktov" ["Hereditary Fixation of Individually Acquired Behavior in Animals and the Origin of Instinct"], *Zhurn. obschei biol.* [*Journal of General Biology*], 1944, *5*: 274.

[52] *Ibid.*, p. 275.

background of emerging hereditary adaptations to the altered environmental conditions may create the illusion of the inheritance of acquired characteristics."[53]

Krushinskii wrote his article in reaction to the publication of a popular pamphlet by V.K. Sudakov, "Secrets of Instinct" (Znanie Publishing House, 1967, 48 pages). The author of this work asserted, with absolutely no grounds, that acquired habits can be inherited under certain conditions. Response to Krushinskii's article came in the form of articles submitted to the editors of *Priroda* [Nature] by Sudakov and Aleksandr Nikolaevich Studitskii. Since Sudakov's article contained nothing new beyond his pamphlet, it was not published. *Priroda* published Studitskii's article as well as commentaries written by the famous specialist on problems of genetics and breeding, Dmitrii Konstantinovich Beliaev. Both items were presented under a single heading "Conditioned Reflexes are not Inherited."[54] Studitskii entitled his article "Pavlov and the inheritance of acquired experience." He included passages from Pavlov's lectures ("Clinical Environments" Vol. I, pp. 616-618 and Vol. III, p. 119) in which Pavlov stated in a general and hypothetical manner that "reflexes were originally conditioned, and later became fixed and unconditioned." He also included Pavlov's opinions concerning the unity of structure and function. The latter observations were quite sound, but bore no relation to the question at hand. In an attempt to attribute to Pavlov a belief in the inheritance of acquired reflexes, Studitskii used an effective polemic method. He quoted Pavlov's words, "Geneticists insist that no acquired traits are inherited. Using sperm from an aggressive male dog, we artificially inseminated a bitch which possessed a well-established passive-defensive reflex." The reader expects that further information would be included concerning the behavior of the progeny, but this is not forthcoming. Instead Studitskii asked, "May we not conclude from these words that this experiment was carried out to confirm the thesis of the inheritance of acquired experience?" In actuality, Pavlov's words indicate that he had set up this experiment to elucidate the question of whether or not the results of acquired experience are inherited. Besides Pavlov's results, Studitskii recounted various works on immunity, tolerance, transplantation, and regeneration which had no bearing on the question of the inheritance of acquired behavioral traits.

In his concluding remarks Beliaev reproduced in brief the history of the debate over the inheritance of acquired characters, especially as it developed in the Soviet Union. He reminded us that the promises made by the supporters of this inheritance to raise highly productive forms of crop plants in a very short time ended in failure and that the successes of the

[53] Leonid Viktorovich Krushinskii, "Nasleduiutsia li uslovnye refleksy?" ["Are Conditioned Reflexes Inherited?"]. *Priroda* [*Nature*] 1968, *no. 1:* 120-123.

[54] *Priroda* [*Nature*], 1968, *no. 11:* 118-123.

geneticists showed indisputably the nonheritability of acquired traits. Turning specifically to the well-established fact that acquired conditioned reflexes are not inherited, Beliaev gave an example which he thought particularly striking. "For the fate of an individual living in a varied environment that changes over time, the inheritance of conditioned reflexes established by their parents would be a tragedy of the highest degree. They would be born with the accumulated behavioral characteristics of their parents, behavior adapted precisely to fit concrete conditions of the parents' lives, but completely unsuited or even harmful in the conditions under which the offspring live." Beliaev explained further that Pavlov's words could be interpreted from the contemporary point of view not as an assertion of the inheritance of acquired conditioned reflexes, but as a theory of the substitution of conditioned-reflex reactions by unconditioned ones. Even if it is necessary to admit that Pavlov mistakenly accepted the inheritance of acquired reflexes as real, his opinion should not influence the contemporary treatment of this question.

Does the Soma have an Effect on Inheritance in Foreign Gametes and Zygotes?

At the base of the hypothesis of the inheritance of acquired characters lies the assumption that the altered soma can have a formative effect on the germ cells, changing them in such a way that the generation developing there from, will possess [similar] alterations in their soma. In order to test this hypothesis of somatic induction, it was quite natural to attempt to create experimentally a system whereby the soma possessed one set of hereditary traits and the germ cells belonged to an organism with different hereditary traits. The techniques of germ cell or sex gland transplantation made possible the creation of such a system.

Before turning to experiments of this type, it should be mentioned that transplantation of the gonads or ovicells is not required to create a system where soma and germ cells have different genotypes. Such systems are regularly produced in nature and can be reproduced in breeding experiments. Laboratory and natural experiments of this kind yield uniformly negative results on the question of the soma of one genotype influencing the germ cells of another genotype.

These considerations have been expressed repeatedly in general terms. Wilhelm Johannsen, in particular, wrote, "The whole of Mendelism, especially the important fact that segregating genes always reappear in the gametes as indivisible entities and in a theoretically determined numerical relationship, shows that gene segregation during fertilization is not influenced by the phenotype as a whole." [1] This same idea was expressed in the several editions of Edwin G. Conklin's book. [2]

We might refer to any hybridization of forms differing, for example, in coloration traits: peas with yellow or green seeds (Mendel's experiment); black or brown mice (Guyénot's experiment, fig. 5). With peas, yellow seed color is dominant over the green, and therefore in the first hybrid genera-

[1] Wilhelm Johannsen, *Elemente der exakten Erblichkeitslehre*, (3rd ed.; Jena: Gustav Fischer, 1926), p. 658.

[2] Edwin Grant Conklin, *Nasledstvennost' i sreda* [*Heredity and the Environment*], trans. from 5th English ed. by Iu. A. Govseev, ed. and preface by M.M. Zavadovskii (Moscow-Leningrad, 1928), pp. 255-256 [5th ed., Princeton: Princeton University Press, 1923].

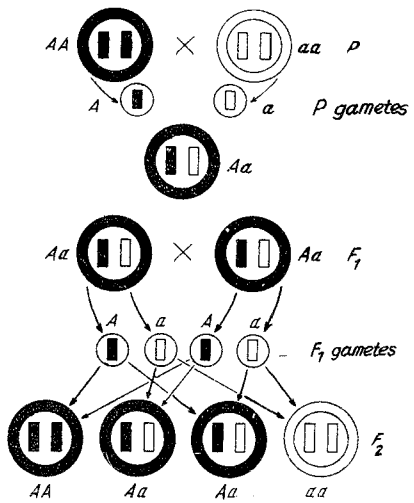

Figure 5. Diagram of a monohybrid cross. Explanation in text.

tion (F_1) all the plants will have yellow seeds. In mice, black fur coloration dominates over brown, and hybrids of the first generation will be black. If the somatic characteristics of such heterozygous organisms had a significant influence on the germ cells developing in them, then recessive forms, for the given examples, green peas and brown mice, would not reappear in the second generation F_2 with pure recessive coloration. Both the above recessives, however, reappear in the F_2 generation in a constant ratio, rendering on the average ¼ of the entire number of second generation individuals. In the accompanying diagram, which is reproduced in one or another variant in all elementary textbooks, the black and white circles represent the soma possessing a dominant and recessive trait, respectively. The black and white rectangles represent the corresponding chromosomes carrying the dominant (A) and recessive (a) genes. In the heterozygote (Aa), which has the dominant phenotype (soma), half of the developing germ cells (eggs or sperm) carry a dominant gene and half a recessive one. The latter are not affected by the dominant soma and participate in an unaltered form in the formation of ¾ of the second generation, which includes the ¼ of this generation which is homozygous for the recessive gene and reproduces the phenotype of the homozygous recessive parent (aa).

These facts became known at the turn of the century upon the rediscovery of Mendel's laws. They were continually corroborated in an ever increasing number of plants and animals. Nonetheless, somatic induction was long considered possible, and to check the possibility of its existence,

scientists performed transplantation experiments. In the chapter on Paul Kammerer's work we discussed his experiments which involved ovicell transplantations from a normal salamander to a female of altered coloring due to soil coloration.

This idea was not new, nor was it originally Kammerer's. A similar experiment was probably first performed in the 1890s by W. Heape.[3] Within 32-48 hours after mating a female albino-angola rabbit with a male of the same breed, Heape extracted fertilized eggs and transferred them to the oviduct of a female of the Belgian variety (pigmented, short-haired). In several cases the transplanted eggs became implanted and the development of the fetus was concluded normally. The rabbit offspring possessed angola traits (long, white hair).

William E. Castle and John C. Phillips, authors who later carried out analogous experiments on guinea pigs, concluded from Heape's experiments that "the foster-mother, indeed, seems not to have influenced the inheritance any more than the corn supplied to cattle determines their breed characters."[4]

It is possible to object to Heape's experiment on the grounds that he dealt with eggs which were already fertilized and which had begun to divide. It is possible that the transplantation of immature ovaries would yield a different result, since in this case the developing eggs would experience the influence of the recipient mother before fertilization and the embryo should in turn be subject to its influence.

One of the first to conduct such an experiment was V. Magnus.[5] He transplanted ovaries from female albino rabbits to a black female and five months later paired her with an albino male. In the first litter one of the young was black and the other albino. The recipient female died during her second pregnancy. Of the fetuses removed from her womb, two were dark colored and five were pink, considered to be albino. Magnus supposed that all the progeny originated from the transplanted ovaries, but it is most likely that the fetuses developed from regenerated as well as transplanted ovaries. In any case, Magnus's experiments cannot serve as evidence for somatic induction.

Before they had been thoroughly analyzed, the results of C.C. Guthrie's experiments, which were published almost simultaneously [with

[3] Walter Heape, "Preliminary Note on the Transplantation and Growth of Mammalian Ova Within a Uterine Foster-Mother," *Proc. Roy. Soc. London,* 1890, *48:* 457-458; "Further Note on the Transplantation and Growth of the Mammalian Ova Within a Uterine Foster-mother," *ibid.,* 1898, *62:* 178-183.

[4] Ernest Castel and John Charles Phillips, *On Germinal Transplantation in Vertebrates, Carnegie Inst. Wash, Publ. no. 144,* (Washington, D.C.: 1911), p. 2.

[5] V. Magnus, *Norsk. Mag. f. Laegeviedensk. Christiania,* 1907, 5S., 5: 1057-1071. Cited according to Castle and Phillips (n. 4).

Magnus's], were considered persuasive evidence of somatic induction.[6] Black and white chickens were used for the experiments. A control cross of white chickens mated with each other yielded eighteen white chicks. A control cross of black chickens mated with each other yielded thirteen black chicks with light breast and throat. These crosses already indicated that the black chickens were not purebred. Two black hens (B_2 and B_3), after being sterilized, received ovary transplants from white hens. Hen B_2 was then paired with a white rooster and hen B_3 with a black. Nine white and eleven spotted chicks (white with black spots on the head, back, and wings) were obtained from hen B_2. Hen B_3 yielded four black chicks with a light chest and throat and two black with white legs. Two sterilized white hens (W_2 and W_3) received ovary transplants from black hens. W_2 was mated with a white and W_3 with a black rooster. Three all-white chicks, one white with black spots, and one black chick were obtained from W_2; white W_3 produced twelve white chicks with black spots. These results all testify not to the presence of somatic induction, but to the impurity of the original material and the failure of a complete removal of the original ovaries from the recipient hens.

In a check of Guthrie's experiments, Charles B. Davenport confirmed that the chick ovary, upon removal, is easily regenerated and that in transplant experiments with foreign ovaries at least some of the offspring come from eggs from regenerated original ovaries.[7]

Castle and Phillips made a further attempt, this time using guinea pigs, to test for somatic induction. Of several dozen females with transplanted ovaries, only one produced offspring that we can consider as having developed from the eggs of the implanted ovaries.

Castle and Phillips described this experiment in the following way. The albino female (no. 27), possessing transplanted ovaries from a "pure-black" of unknown genotype, was paired with an albino male (no. 654) and "produced two females. One (no. 1970) was black with a few red hairs and the other (no. 1969) was also black, but had some red hair and a white right foreleg." She then [upon second pregnancy] produced a male that was mostly black with some red hair. Later the female (no. 27) "died of pneumonia [in her third pregnancy] with three full grown male young in utero. . . . Like the other three young, they were black, but with a few red hairs among the black. They bore no white hairs." The albino male (no. 654), when paired with a pure-black female, sired offspring which were all black with red hair. "This result shows," concluded Castle and Phillips, "that the red hairs found on the six young of the grafted albino were due, not to

[6] C.C. Guthrie, "Further Results of Transplantation of Ovaries in Chickens," *J. Exper. Zool.,* 1907, *5:* 563-576.

[7] Charles Benedict Davenport, "The Transplantation of Ovaries in Chickens," *J. Morphol.,* 1910, *22:* 111-122.

foster-mother influence of the grafted albino, but to influence of the male parent. The young of the grafted mother were exactly such in color as the black guinea pig which furnished the graft herself might have been expected to bear had she been mated with male 654. . . . The white foot borne by one of the young forms no exception to this statement. Spotting characterized the race of guinea pigs from which the father came. He was himself born in a litter which contained spotted young, whereas neither the pure-bred black race that furnished the graft nor the albino race that received it was characterized by spotting." Undoubtedly Castle and Phillips's experiment was not carried out with sufficient rigor, since the black female donor (the true mother of the offspring under study) should have been a carefully verified homozygote. Castle and Phillips correctly considered that their experiment "gave no indication of foster-mother influence in their coloration."[8]

Petr O. Sakharov and N.I. Feiginson elucidated the results of Castle and Phillip's work in a wholly nonobjective fashion. Sakharov described the experiment thus: The white female with an ovary transplanted from a black guinea pig was paired with a white male and in the first two litters yielded black offspring with a certain amount of red hair. In the third litter her three offspring, which were not carried to term, "had hair of mixed black and gold coloration, in which the latter was dominant.[9] Consequently, the influence of the mother's coloration on the coloration of the embryos was revealed here. . . . It is interesting that Sinnot and Dunn denied the influence of the mother on the coloration of the offspring, . . . and simply omitted the drawings of the guinea pigs which proved the influence of the mother's body."[10] In other words, Sakharov accused the authors of this famous genetic text of negligence in setting forth Castle and Phillips's data. Feiginson wrote on the same topic and referred not only to Edmund W. Sinnot and Leslie C. Dunn, but to Francis A.E. Crew and Petr Fomich Rokitskii, the latter of whom had reproduced a diagram from Crew's text in his own genetics textbook. According to Feiginson, the offspring of the first and second litters in Castle and Phillips's experiment "had lighter hair as well as black hair. . . . But the influence of the white female was particularly striking in the third generation. The offspring turned out to be not black, nor even brown, but spotted. They had light and dark spots. In other words, Castle and Phillips's experiment proves the exact opposite of that which Rokitskii, Crew, Sinnot, and Dunn claim."[11]

[8] Castle and Phillips (n. 4), pp. 9–10.

[9] Castle and Phillips were actually speaking of a small quantity of red hair.

[10] Petr O. Sakharov, *Nasledovanie priobretaemykh svoistv* [*The Inheritance of Acquirable Characters*] (1952), p. 213.

[11] N.I. Feiginson, *Nasledovanie priobretaemykh svoistv* [*The Inheritance of Acquirable Characters*] (1951), p. 16.

As was pointed out, Castle and Phillips themselves considered that their results argued against somatic induction. In his last book Kammerer, who can hardly be suspected of wanting to make the results of an experiment that denied somatic induction any more explicit than it already was, came to the same conclusion regarding Castle and Phillips's experiment. "Castle and Phillips," wrote Kammerer, "transplanted the ovary of a black guinea pig into the body of a white specimen; after this, they crossed the latter with a white male. In spite of this, the two young born were purely black. . . . The 'black' ovary evidently does not 'whiten' in the body of a white female."[12]

It is precisely this conclusion which is illustrated by the photographs in Sinnot and Dunn's textbook and by the diagrams in Crew's and Rokitskii's texts. For the sake of appearance called for by pedagogical purposes, Sinnot and Dunn discarded the portion of the drawings depicting those guinea pigs of the third litter of female no. 27 that had the most red hair (though not white spots), and Crew and Rokitskii provided only a schematic diagram. The summaries of Castle and Phillips's work are just as schematic in a book by Conklin, for whom the fundamental nature of the results was also quite clear.[13]

Later, Berthold P. Wiesner devoted research time to the same question. He improved the methodology of the experiments in several ways. He removed the ovaries from rats, together with the proximal section of the fallopian tubes so that in the event of a regeneration of the ovaries, eggs from them could not find their way to the uterus. After this, an ovary from a donor of a different color than the recipient was transplanted to the uterine cavity of the sterilized female. Ovaries were transplanted from a pigmented female to a white one and vice versa. In the first case, when the female was mated with an albino male, an albino young was born. In the second case one pigmented and two albino young were born. Consequently the females from whom the ovaries were taken must have been heterozygous. In experiments where ovaries were transplanted from albinos to pigmented rats, offspring were born with coloration corresponding to that of the donor's genotype. Wiesner concluded, "No influence of the foster-mother on the pigmentation of the offspring is revealed."[14]

W. Harms carried out reciprocal ovary transplantations between individuals of different species of *Oligochaetae* [earthworms and their freshwater and tidal water relatives] (*Helodrilus caliginosus* and *Lumbricus ter-*

[12] Paul Kammerer, *Neuvererbung oder Vererbung erworbener Eigenschaften* (1925), p. 93. [For English passage, see Kammerer (chapter 17, n. 17), p. 141.]

[13] Conklin (n. 2), pp. 254–255.

[14] Berthold P. Wiesner, "Die Funkionsfähigkeit autophor transplantierter Ovarien bei Ratten," *Arch. mikr. Anat. und Entw.-mech.*, 1923, *99*: 147

restris, Lumbricus rubellus and *Helodrilus longus, Helodrilus longus* and *Octalasium cynaneum*). He established that the soma of the "recipient mother" did not have any effect on the characteristics of the offspring which developed out of eggs from the transplanted gonads. The second report on this work included data concerning the transplantation of ovaries of the crested triton (*Triton cristatus*), [a salamander] which lays white eggs, to sterilized females of the alpine triton (*Triton alpestris*), which lays pigmented eggs. The alpine tritons which underwent this operation laid white eggs, that is, their soma bore no specific influence on the transplanted ovaries.[15]

Berthold Klatt conducted sterilization and ovary transplantation experiments on the caterpillars of the gypsy moth (*Lymantria dispar*), one variety of which produces black caterpillars and another of which produces yellow caterpillars.[16] In a hybridization experiment Klatt established that black coloration in the caterpillars is dominant to yellow. He transplanted ovaries from the recessive variety to the dominant variety. From the nine moths that had received successful transplants, he obtained four hundred caterpillars. All were yellow, which showed that there was no somatic induction in this case.

Thus, we may consider that the question of somatic induction had been conclusively answered by the beginning of the twenties. During the forties and the beginning of the fifties in the Soviet Union, however, further gonad transplantation experiments were carried out to address this question. At the International Genetics Symposium in Japan, Khila F. Kushner gave a summary of the work published during those years.[17] First and foremost he noted the work of I.A. Baryshnikov and co-workers.[18] They had transplanted ovaries from a white rabbit to a black female rabbit. After mating with a black rabbit, the recipient gave birth to one black and one white rabbit in each of the first two litters and six black rabbits in the next two litters.

[15] W. Harms, "Überpflanzung von Ovarien in eine fremde Art I Mitt. Versuche an Lumbriciden," *Arch. Entw.-mech.*, 1912, *34:* 90-131; "II Mitt. Versuche an Tritonen," *ibid.*, 1913, *35:* 748-780.

[16] Berthold Klatt, "Keimdrüsentransplantationen beim Schwammspinner, Ein experimenteller Beitrag zur Frage der Vererbbarkeit erworbener Eigenschaften," *Z. Indukt. Abstammungs- und Vererbungslehre*, 1919, *22:* 1-50.

[17] Khila Faivilovich Kushner, "Vliianie metabolicheskikh faktorov na nasledstvennost' zhivotnykh" ["The Influence of Metabolic Factors on Inheritance in Animals], *Agrobiologiia* [*Agrobiology*], 1957, *103:* 19-35.

[18] I.A. Baryshnikov, M.G. Zaks, and E.F. Pavlov, "Vliianie materinskogo organizma na okrasku shersti u potomstva krolikov v usloviiakh gomotransplantatsii iachnikov" ["The Influence of the Maternal Organism on Hair Coloration in the Offspring of Rabbits Under the Condition of Ovary Transplantation"], *Dokl. AN SSSR* [*Reports of the Academy of Sciences of the USSR*], 1950, *72:* 1123-26; *Izv. AN SSSR, seriia biol.* [*News of the Academy of Sciences of the USSR, Biology Series*], 1950, *no. 6:* 77-95.

Despite assurances that during the work measures were taken to prevent the regeneration of the ovaries removed from the black rabbit, one must recognize that this regeneration did take place and that the different colored offspring arose from both the original and transplanted ovaries, or alone from the ovaries of the black rabbit, in which [incidentally] the heterozygous state had not been ruled out. Kushner tried to parry the logical suggestion of regeneration of the removed ovaries in his experiment by reference to E.F. Pavlov's experiments.[19] Pavolv as well as Guthrie had performed similar experiments on chickens, also without verifying the homozygous state of their subject, and obtained spotted chicks, which proved nothing in either experiment. In any case, the absence of regeneration in Pavlov's experiment would have no bearing on the question of regeneration of rabbit ovaries in Baryshnikov's experiments.

The possibility of the influence of the mother's soma on genotypical features of offspring was also investigated by means of intervarietal transplantations of fertilized eggs or early embryos. A.D. Kurbatov reported the results of such transplantations in rabbits.[20] Female rabbits of a pigmented variety, Rex, were used as donors. Females of the White Giant variety received the transplants and were paired with Rex males. The twenty-four rabbit offspring were similar in color to the parents from whom the eggs and sperm were derived, that is, they possessed the coloring characteristics of the Rex variety. Only in one instance, in the transplantation of a zygote from a female Chinchilla rabbit, did the author note a change in the coloration of the rabbit offspring in the direction of the "recipient mother," but he failed to give a detailed description. Kurbatov cited data in another article that showed that there were no genetic changes in individuals developing from transplanted zygotes.[21] Finally, in yet another work, Kurbatov reported an instance in which a male Chinchilla rabbit whose embryonic development took place in a female of the White Giant variety kept the coloration typical of his variety.[22] Upon mating this

[19] E.F. Pavlov, "Nasledovanie okraski kur v usloviakh retsiproknoi peresadki iaichnikov" [The Inheritance of Coloration in Chickens Following Reciprocal Ovary Transplantation"], *Izv. AN SSSR* [*News of the Academy of Sciences of the USSR*], 1951, *no. 10:* 879-884.

[20] A.D. Kurbatov, "Opyty po mezhporodnoi peresadke oplodotvorennykh iaitsekletok u krol'chikh" ["Experiments with Intervarietal Transplantation of Fertilized Ovicells in Female Rabbits"], *Tr. Pushkinskoi n.-i. lab. razvedeniia c.-x. zhivotnykh* [*Transactions of the Pushkin Scientific Research Laboratory for the Breeding of Agricultural Animals*], 1950, *no. 4.*

[21] A.D. Kurbatov, "Izmenenie nasledstvennosti i povyshenie zhiznennosti potomstva putem mezhporodnykh peresadok iaitsekletok '["Changes in Heredity and Increase in Vitality of Offspring Through Intervarietal Ovary Transplantation"], *Usp. covrem. biol.* [*Successes of Contemporary Biology*], 1951, *32.*

[22] A.D. Kurbatov, "Rezkoe izmenenie nasledstvennosti krolikov, razvivshikhsia v organizme inoporodnoi materi" ["Significant Change in Inheritance in Rabbits that Develop in the Body of a Mother of a Different Species"], *ibid.*, 1952, *33:* 466-471.

individual with a female Chinchilla rabbit twenty-three of the thirty-five young produced had Chinchilla coloration and the rest were light grey or ermine colored. Instead of concluding that the material used for Kurbatov's original implantation was heterozygous, that is, unsuitable for the solution of the question posed, Kushner referred to this instance as a proof of somatic induction.[23]

In discussing the negative results of intervarietal zygote transplants, Kushner offered the suggestion that in mammals the placenta acts as a barrier to substances which might cause the fetus to change its varietal characteristics in the direction of the "recipient mother."[24] Somewhat earlier, concerning the experiments of Baryshnikov and co-authors, Kushner had written that they "could not be explained any way except as the result of the influence of the recipient mother, a black rabbit, on the ovicells transplanted from an albino white rabbit."[25] In other words, Kushner arbitrarily assumed the presence of an obstacle in the form of a placental barrier only in those instances where no influence of the soma on foreign ovicells was discovered.

A.I. Lopyrin, N.V. Loginova, and P.A. Karpov carried out intervarietal zygote transplantation studies. In the published report of their experiments, they concluded that no coloration changes in lambs in the direction of the "recipient mother" had taken place. The changes in the described external characters were so vague that the authors themselves were inclined to attribute them to natural variations and the impure nature of the material used in the experiment.[26] In another zygote implantation experiment in sheep, F.M. Mukhamedgaliev and R.B. Abil'dinov recently obtained clearly negative results. They used coarse-haired, fat-tailed sheep as recipients into which they transplanted eggs at the two to six-blastomere stage taken from Kazak fine-fleeced sheep which had been mated with rams of the same breed. All five lambs obtained in the experiment "were typical fine-fleeced sheep both in external appearance and in fleece quality. The fat-tailed recipient mothers had no noticable effect on... the lambs which developed from the implanted zygotes."[27]

[23] Kushner (n. 17), p. 24.

[24] In particular, the article of A.V. Kvasnitskii, "Opyt Mezhporodnoi peresadki iaitsekletok" ["Experiment in Intervarietal Ova Transplantation"], *Sov. zootekhnik* [*Contemporary Livestock Specialist*], 1951, *no. 1:* 36–42.

[25] Kushner (n. 17), p. 21.

[26] A.I. Lopyrin, N.V. Loginova and P.L. Karpov, "Opyt mezhporodnoi peresadki zarodyshei u ovets" ["Experiment in Intervarietal Embryo Transplantation in Sheep"], *Sov. zootekhnik* [*Contemporary Livestock Specialist*], 1950, *no. 8.*

[27] F.M. Mukhamadgaliev and R.B. Abil'dinov, "Opyt mezhporodnoi peresadki zigoty u ovets" ["Results of Intervarietal Transplantation of Zygotes in Sheep"], *Genetika* [*Genetics*], 1968, *4:* 68. See also the book by Mukhamedgaliev and Abil'dinov, *Mezhporodnaia peresadka zigoty i ee geneticheskie aspekty* [*Intervarietal Zygote Transplantation and its Genetic Aspects*] (Alma-Ata: 1971).

Along with these experiments which explored the possible influence of foreign soma on zygotes or on the developing ova, scientists also attempted to influence the male gametes by foreign soma. The idea for such experiments belongs to Boris Grigorievich Novikov, who experimented on chickens and ducks and first reported his results in 1951. A summary of his experiments appeared in a paper in 1966.[28] Novikov castrated one- to five-day-old chicks of the White Leghorn variety and transplanted into them several testicles from chicks of the Rhode Island Red variety of the same age. Conversely, castrated Rhode Island Red chicks received testicle transplants from Leghorns. In one to two years sperm taken from the artificially developing testicles was used to inseminate artificially hens of the same variety as the original testicle donor. The summary paper briefly noted that in offspring obtained from these chickens "various changes in plumage coloration and other somatic features emerged." A still greater range of variability was observed in subsequent generations, especially with the use of sexual hybridization. Thus, upon crossing Rhode Island Reds with a white rooster, which had been obtained from a Leghorn egg fertilized by sperm from Leghorn testicles developed in a Rhode Island Red individual, chickens of the following phenotypes resulted: white with crown-shaped combs, black with crown-shaped and with leaf-shaped combs, and gray-striped and Andalusian colorations.

Novikov carried out transplantations in an analogous fashion upon ducks. He transplanted testicles from White Peking ducks to ducks whose parents had the coloration of the wild duck and vice versa. Of the ducks from White Peking eggs, which had been obtained through artificial insemination with sperm from White Peking testicles developed in the body of wild ducks, some had no changes from the white plumage coloration while others displayed various changes in coloration of plumage, beak, and legs. Changes in plumage coloration and other features were also obtained with reciprocal transplants. Novikov at first interpreted these results as manifestations of vegetative hybridization, that is, somatic induction.[29] In a paper read in 1966, however, he specifically noted that "in duck and chicken offspring obtained from females artificially inseminated with sperm from testicles that had developed in the body of a fowl of another breed, the variability of characteristics took on a character other than that found in various combinations of crossing of the original forms."[30] Novikov concluded that the action of a foreign soma induced

[28] Boris Grigorievich Novikov, "Eksperimental'noe izmenenie porodnykh priznakov u domashnei ptitsy" ["Experimental Alteration of Varietal Characters in Poultry"], *Tr. XIII Vsemirnogo kongressa po ptitsevodstdu* [*Transactions of the XIII World Congress on Poultry-farming*] (Kiev: 1966), pp. 98–102.

[29] Boris Grigorievich Novikov, *Opyty vegetativnoi gibridizatsii u ptits* [*Vegetative Hybridization Experiments on Poultry*] (Kiev: 1953).

[30] Novikov (n. 28), p. 100.

"physico-chemical changes in the nucleic acids of spermatozoids," which, obviously, should be understood as his acceptance of a nonspecific mutagenic influence. In other words, there can be no talk of somatic induction in Novikov's experiments. The results themselves, however, need confirmation under more precise experimental conditions and recording of results, since the manner in which traits segregated suggests the possibility of uncontrolled mating.

Results recently reported by Novikov have been verified by Jacques Benoit and E. Brard, who used an improved method.[31] They transplanted testicles from 2-, 16-, and 23-day-old chicks of the White Wyandotte variety (W) into the testicles of eight to eleven-month-old roosters of the Rhode Island Red variety (RIR) that had previously been exposed to x-rays at a dosage of 1800 roentgens in order to halt multiplication and differentiation of spermatogenic cells. In the control experiment (exposure to x-rays without implantation of foreign testicles) roosters developed normally and displayed sexual activity, but were completely sterile. Histological sections of their testicles revealed empty seminal vesicles and differentiated interstitial endocrine tissue. Two to five months following the transplantation of testicles the experimental roosters were mated with RIR or W hens. Offspring (25 chicks) were obtained only from RIR hens. The almost completely white plumage of the F_1 hybrids, i.e., ♂ RIR [W] × ♀ RIR, was identical to that normally obtained in F_1 hybrids, i.e., ♂ W × ♀ RIR. Crossing the F_1 hybrids i.e., ♂ RIR [W] × ♀ RIR, with each other yielded in the F_2 generation three coloration types corresponding to Mendelian laws of segregating traits. Thus, Benoit and Brard's experiments demonstrated that somatic induction does not occur with the transplantation of foreign testicles.

[31] Jacques Benoit and E. Brard, "Greffes interrraciales de testicules chez les Gallinacés. 'Testotestes' fertiles obtenus par greffe de testicules de poussins Wyandotte blanc dans les testicules stérilisés par les rayons x de coqs Rhode Island Red," *Compt. Rend. des Séances de la Soc. Biol. et de ses Filiales*, 1968, *162:* 838–842.

CHAPTER 19

So-Called Vegetative Hybridization

The technique of grafting part of one plant onto another, known to gardeners from earliest antiquity, has served practical goals as well as the study of the interaction between stock and scion. Data from the past concerning the mutual formative effect of the stock and the scion are, as a rule, completely unreliable. Investigators during the seventeenth and eighteenth centuries described examples, such as the flowering and fruiting of pear trees grafted to ash trees, the change in the color of the orange pulp with the grafting of oranges onto pomegranates and a darkening of the flowers of the rose when grafted onto an oak.[1]

Belief in the possibility of such effects was widespread and even found expression in the poetry of the eighteenth century:

To an ash, on purpose,
A rose was grafted.
The rose did not fade—
It was the same flower
And yet there was a change:
The scent was gone! . . .

—I.I. Dimitriev
[trans. Noel Hess]

Darwin discussed in detail the results of grafts of various plants, beginning with *bidzaria,* a chimera of bitter orange and lemon, known since 1667, and Adam's Broom, obtained in 1828 from a graft of *Cytisus purpureus* to *Laburnum vulgare*. He also mentioned grafts to jasmine, ash, filbert, grape, hyacinth, and especially to potatoes.[2] Darwin called phenomena of this type graft hybridizations. Strictly speaking there was no basis for this since the tissue structure of the resulting grafted forms had not yet

[1] Andrei Ivanovich Luss, "Vzaimootnoshenie podvoia i privoia (O roli transplantatsii v selektsii)" ["The Interrelationship Between Stock and Scion: On the Role of Transplantation in Breeding"], *Teoreticheski osnovy selektsii rastenii* [*Theoretical Bases of Plant Breeding*], ed. N.I. Vavilov (Moscow-Leningrad: 1935), vol. I, pp. 689–752.

[2] Charles Darwin, *Izmeneniia domashnikh zhivotnykh i kul'turnykh rastenii* [*Variation of Animals and Plants Under Domestication*], in *Soch.* [*Works*], 1951, *4:* 413–421. [Darwin, *Variation* (New York:1897), pp. 413–424.]

been studied and since not one of the "graft hybrids" known to Darwin had formed seeds so that one could judge the hereditary characteristics arising from the graft. Nevertheless, Ivan E. Glushchenko, in commenting upon the pertinent chapter of volume 4 of Darwin's *Collected Works,* referred unsceptically to Darwin's examples as graft hybrids.[3] Horticulturists, who cited more believable, though not rigorously verified, instances of the influence of one component of a graft on the other, long held the belief not only that changes could be produced with a graft but that they could be fixed by the subsequent sexual reproduction. The Russian horticulturist M.V. Rytov held this view and considered vegetative hybridization to be identical to sexual hybridization.[4]

Studies of the structure of vegetative hybrids began early in this century. At the suggestion of H. Winkler, plants formed by combining parts of plants of different parentage began to be called chimeras.[5] Erwin Baur was particularly insistent on the chimeric character of plants which resulted from grafts.[6]

In line with the purposes of this book we must examine the persuasiveness of the evidence that the characters of "vegetative hybrids" could be transmitted to successive generations through the seeds of such hybrids.

Ivan Vladimirovich Michurin consistently used the term "vegetative hybrids" and even carried on a polemic with those who denied their existence.[7,8] In order to understand exactly what phenomena Michurin took to be vegetative hybridization, Semeon Ia. Kraevoi did a thorough study of those examples used by Michurin.[9] He concluded that in all of the examples where the stock had actually influenced the scion, or vice versa, the changes resulting from the graft were not transmitted to the generation that later developed from the seeds.

An article by Nikolai P. Dubinin and a pamphlet by Sos I. Alikhanian

[3] *Ibid.*, p. 821. [The reference here seems to apply to an article or editorial comment by Glushchenko in Darwin's collected works.].

[4] A.P. Berdyshev, *Mikhail Vasil'evich Rytov. Russkii agrobiolog* [Mikhail Vasil'evich Rytov: Russian Agribiologist] (Moscow: 1951).

[5] H. Winkler, "Über Piropfbastarde und pflanzliche Chimären," *Ber. Dtsch. bot. Ges.*, 1907, 25: 568-76; "Über das Wesen der Pfropfbastarde," *ibid.*, 1910, *28*:116-118.

[6] Erwin Baur, "Pfropfbastarde," *Biol. Chl.*, 1910, *30*:497-514.

[7] See, for example, Ivan Vladimirovich Michurin, *Printsipy i metody raboty* [*Principles and Methods of Work*], in *Soch.* [*Works*], 1948, *1*.

[8] Ivan Vladimirovich Michurin, "Oshibochnoe suzhdenie mnogikh uchenykh issledovatelei po priznaniiu vozmozhnosti iavleniia vegetativnykh gibridov" ["Mistaken Opinions of Many Scientist-Experimenters on Recognizing the Possibility of Vegetative Hybrids], *ibid.*, pp. 388-395.

[9] Semeon Iakovlevich Kraevoi, *Vozmozhna li vegetativnaia gibridizatsiia rastenii posredstvom privivki?* [*Is Vegetative hybridization of Plants Through Grafting Possible?*] (Moscow: 1967), pp. 111-113.

explained Michurin's real attitude toward so-called vegetative hybridization. Michurin assumed that the stock altered the nature of the scion by modifying the role of its hereditary components during development. His followers, however, supposed that the stock actually induced the inheritance of new traits in the scion.[10] Dubinin pointed out that the dozens of "vegetative hybrids" obtained by Glushchenko and Artavazd A. Avakianii were not equivalent to sexual hybrids. Alikhanian showed that it had cost Michurin much effort to rise above the pseudoscientific views of horticulturist A.K. Grell', which predominated at the end of the nineteenth century and which upheld the idea of vegetative hybridization.[11]

In a similar fashion L. Daniel expressed confidence in the existence of true vegetative hybrids and linked vegetative hybridization to the question of the inheritance of acquired characters.[12] He claimed that his research "demonstrates experimentally the validity of Lamarck's hypothesis concerning the inheritance of acquired traits induced by the environment."[13] After Auguste Chevalier had cultivated Daniel's graft hybrids for a prolonged period at the Museum of Natural History in Paris; it became clear, however, that he was working with chimeras, sexual hybrids, and the results of taxonomic errors.[14]

In the works already cited and in his later writings Daniel suggested that the hybrid character of plants which resulted from grafts arose through the fusion of the vegetative nuclei of the various graft components. This process seemed analogous to true hybrids which develop from the fusion of nuclei of the egg and sperm of the individual varieties. At first, Winkler, who based his views on grafts of nightshade to tomato and vice versa, agreed with Daniel. But later, influenced by the critical considerations of Baur, Winkler admitted the chimeric rather than hybrid nature of the forms obtained through grafting. An important argument supporting Baur's opinion was the fact when the fruit-bearing parts of the grafted plants were self-pollinated. The resulting seedlings appeared identical with one or the other of the original plants, i.e., the nightshade or the tomato. William Nielson Jones, author of a survey devoted to these phenomena, noted that the objections to Daniel's [hybridization-through-cell-

[10] Nikolai Petrovich Dubinin, "I.V. Michurin i sovremennaia genetika" [I.V. Michurin and Contemporary Genetics"], *Vopr. filosofii* [*Questions of Philosophy,*], 1966, *no. 6*: 59-70.

[11] Sos Isaakovich Alikhanian, *Teoreticheskie osnovy ucheniia Michurina o peredelke rastenii* [*The Theoretical Basis for Michurin's Doctrine of Plant Variation*] (Moscow; 1966).

[12] L. Daniel, "La variation dans la greffe et l'hérédité des caractéres acquis," *Ann. sci. natur. Bot.*, 1898, *8*: 1.

[13] L. Daniel, "Nouvelles observations sur les hybrides de greffe et l'hérédité chez les plantes greffés," *Rev. Breton. Bot.*, 1924 (1925), pp. 1-70. Cited in an article by A.I. Luss (n. 1), p. 716.

[14] Paul Wintrebert, *Le vivant créateur de son évolution* (Paris: 1962), p. 32.

fusion] theory focussed on "the complete lack of any reliable evidence concerning vegetative fusion of two genetically different cells."[15]

Analysis of the karyotype serves as an important argument in favor of the chimeric nature of forms obtained by grafting. In the tomato the diploid number of chromosomes in vegetative cells is twenty-four, and the haploid number in pollen grains is twelve, whereas in the nightshade they are seventy-two and thirty-six chromosomes, respectively. If the forms Winkler had obtained had been vegetative hybrids, then, according to Daniel's hypothesis, their cells would have revealed ninety-six (that is, 24 + 72) chromosomes each and the pollen would have had forty-eight chromosomes. In fact, the vegetative cells of the "graft hybrids" contained either seventy-two or twenty-four chromosomes, and the pollen grains procured from seedlings which were indistinguishable from nightshade contained thirty-six chromosomes while those from seedlings which were indistinguishable from tomato contained twelve chromosomes. One of the specimens, the seedlings of which were not studied, revealed forty-eight chromosomes in the vegetative cells. Since the phenomenon of somatic reduction is extremely unlikely and has never been observed cytologically, it is natural to suggest that this instance represented not a vegetative hybrid (24 + 72 chromosomes with a successive halving by reduction) but a tetraploid tomato sucker (12 × 4). Nikolai Pavlovich Krenke obtained analogous results working with chimeras of *Solanum lycopersicum* and *S. memphiticum*.[16]

Jones analyzed other more or less well known grafts, such as medlar onto hawthorn, pear onto quince, and peach onto almond. Some people had considered these also as graft hybrids. In all cases detailed microscopic investigation revealed the chimeric nature of the plants. In his detailed survey on the reciprocal relationships between stock and scion, cited above, Andrei Ivanovich Luss also concluded, on the basis of the data in the literature, that no one had succeeded in creating a graft hybrid.

Nonetheless, soon after publication of this article by Luss and the Russian translation of Jones's book in the Soviet Union, publications began to appear which again raised the question of the possibility of obtaining true vegetative hybrids. In 1938 in the journal *Iarovizatsia* [*Vernalization*],

[15] William Nielson Jones, *Rastitel'nye khimery i privivochnye gibridy* [*Plant Chimaeras and Graft Hybrids*], trans. T. Asseeva (Moscow-Leningrad; 1936), p. 37. [The English original was published under the same title (London: Methuen & Co., 1934.]. The fusion of the "formative elements," which "are contained not only in the reproductive organs, but are also present in the gemma and cell tissue of plants" had been suggested by Darwin in a discussion of "graft hybrids" (n. 2), p. 731.

[16] Nikolai Pavlovich Krenke, *Wundkompensation, Transplantation und Chimären der Pflanzen* (Berlin: 1933).

later entitled *Agrobiologiia,* the editor of the journal himself[17] and his co-workers A.A. Avakian,[18] I.E. Glushchenko,[19] V.I. Razumov[20] and others published articles in which they discussed the possibility of producing vegetative hybrids. The ideas they advanced were in part arguments directed against the general principles of contemporary genetics and against the chromosome theory of inheritance in particular. In the following years, Trofim Denisovich Lysenko continually appeared in print with polemical articles upholding the idea of vegetative hybridization. Lysenko wrote, "The scientific term 'chimera' denotes those organisms whose tissues apparently consist of the mechanical combination of tissue from two varieties. In fact, such so-called chimeras can be viewed as manifestations of the phenomenon of mosaic inheritance where one part of the organism possesses the characters of one of the 'parents', the other part from the other 'parent'. An analogous case would be a piebald or spotted cow in which one patch of hair has the coloration of the mother and another patch has that of the father. But who would think of calling a spotted cow a chimera?"[21] In that same year, 1940, Vera Vladimirovna Khvostova wrote an article elucidating this question with data cited from the latest literature and evaluating those proposals which equated phenomena of grafting with true hybridization. She concluded that "the assumption that vegetative hybridization is equivalent to hybridization through sexual reproduction is incorrect."[22]

Soon afterwards, an article appeared in which Lysenko asserted: "In the joining of two young plants of different varieties through grafting, it seems as if a transfer of hereditary characteristics takes place from one component to the other. If seeds are taken from such grafts, the same thing

[17] Trofim Denisovich Lysenko, "Mentor—moguchee sredstvo selektsii" ["Mentor—The Most Powerful Means of Breeding"], *Iarovizatsiia* [*Vernalization*], 1938, *no. 3:* 35–44.

[18] Artavazd Arashakovich Avakian, "Vegetativnaia gibridizatsiia kartofelia" ["Vegetative Hybridization of Potatoes"], *Iarovizatsiia* [*Vernalization*], 1938, *no. 3:* 83–85.

[19] Ivan Evdokimovich Glushchenko, "Rol' pitaniia v izmenenii prirody kartofelia" ["The Role of Nutrients in Altering the Nature of Potatoes"], *Iarovizatsiia,* [*Vernalization*], 1938, *no 3:* 86–90. See also I.E. Glushchenko, *Vegetativnaia gibridizatsiia* [*Vegetative Hybridization*] (Moscow:1948).

[20] V.I. Razumov, "Izmenenie nasledstvennykh svoistv kartofelia putem privivki" ["Changes in Hereditary Traits of Potatoes Through Grafting"], *Iarovizatsiia* [*Vernalization*], 1939, *no. 1:* 100–109.

[21] Trofim Denisovich Lysenko, "O putiakh upravleniia rastitel'nym organizmom" ["On Methods of Managing the Plant Organism"], *Vestn. AN SSSR* [*Communications of the Academy of Sciences of the USSR*], 1940, *no. 6:* Cited in *Agrobiologiia* [*Agrobiology*], (6th ed.; Moscow: 1952), p. 312.

[22] Vera Vladimirovna Khvostova, "Problema genotipicheskogo vliianiia pri privivkakh i transplantatsiiakh" ["Problems of Genotypic Influences in Grafts and Transplants"], *Zhurn. obshchei biol.* [*Journal of General Biology*], 1940, *1:* 469.

occurs in the seed generation as usually takes place in sexual hybridization. . . . At the present time there are hundreds of examples in which, as the result of a graft of two plant organisms of different varieties, a third, hybrid organism is obtained. The hybrid here is created by an exchange of genetic materials between the graft components."[23]

Two years later Lysenko refuted the generally accepted method of hybridization for the study of inheritance. "To study the inheritance of a given organism," he asserted, "one need not breed plants and animals with different inheritance."[24] Repeatedly he declared, "When . . . during recent years a method was found to produce vegetative hybrids which behave in the seed generation exactly as normal sexual hybrids, geneticists could no longer come up with concrete objections. They simply denied these facts and sometimes called them experimental errors. But for fear of obtaining vegetative hybrids, they have resisted repeating for themselves these experiments."[25] In Lysenko's opinion, vegetative "hybrids" were formed not through the fusion of vegetative nuclei as Daniel thought, but through the influence of substances transmitted from one component of the graft to the other. N.I. Feiginson repeated similar and equally unfounded opinions.[26,27]

[In opposition to these claims] Kraevoi published in 1967 a book which contained his own [critical] investigations, which began in the 1930s, and other relevant data drawn from the literature.[28] The works of Brix, Rick, Stubbe, Böhme, Zhebrak, Rzegocinska, and others, carried out subsequent to Kraevoi's research, also established the erroneous nature of claims of the production of vegetative hybrids.

K. Brix repeated grafting experiments on the same varieties of tomato as those which, according to Glushchenko (1948), produced vegetative hybrids. He established that one component of the graft did not change to the slightest degree in the direction of the other component, let alone form a true vegetative hybrid.[29] In Brix's opinion, the results described by Glushchenko and other experimenters who asserted the possibility of

[23] Trofim Denisovich Lysenko, in *Vestn. AN SSSR* [*Communications of the Academy of Sciences of the USSR*], 1941, *no. 1*. Cited in the book *Agrobiologiia* [*Agrobiology*] (n. 21), pp. 364-365.

[24] Trofim Denisovich Lysenko, *O nasledstvennosti i ee izmenchivosti* [*On Inheritance and its Variability*] (Omsk: 1943). Cited in *Agrobiologiia* [*Agrobiology*] (n. 21), p. 433.

[25] *Ibid.*, p. 455.

[26] See the genetics text by N. I. Feiginson (Isd. MGU [Moscow State Univ. Publishers], 1955), p. 242.

[27] *Ibid.*, p. 243.

[28] Kraevoi (n. 9).

[29] K. Brix, "Untersuchungen über den Einfluss der Pfropfung auf Reiz und Unterlage und die Möglichkeit einer Übertragung eventueller Veränderungen auf die Nachkommen," *Pflanzenzucht*, 1952, *31:* 261-288.

producing vegetative hybrids, depended on whether or not they had included a control in their experiments. If a control was included, as was done in particular by Charles M. Rick, one could then ascertain that all the changes produced by the graft were nonhereditary in nature.[30]

Hans Stubbe's investigations, which refuted Lysenko's assertions,[31] were particularly important. On the basis of 2,455 grafts which he performed on different varieties of tomato to clarify the mutual influence of stock and scion Stubbe concluded, "not one instance produced evidence of the transfer of genetically conditioned traits from one of the graft components to the other in the graft generation."[32] He studied the traits of 15,560 progeny of 351 grafted plants and observed no influence whatsoever of the scion on the stock. Segregation of traits in the offspring of heterozygous graft components and in ungrafted control plants took place in accord with normal monohybrid crossings. From the data of his experiments carried out between 1949 and 1952 Stubbe concluded, "Investigations of the problem of vegetative hybridization of plants, carried out on a large quantity of material and in the course of a prolonged period of time, gave me no evidence of the existence of this phenomenon."[33] An abstract of this article appeared in *Botanicheskii Zhurnal* [*The Journal of Botany*].[34]

Nikolai Tsitsin and M.Z. Nazarova[35] reported the results of grafting the tomato plant onto the tomato tree (*Cyphomandra betaccae*). Some of the fruit differed in appearance from that of the Bizon variety used as a scion. Among the seedlings from these fruits one displayed leaves similar to those of the Mikado variety of tomato. In discussing these data, Kraevoi correctly noted that the appearance of such specimens could be explained in a variety of ways and in any case could not serve as proof of vegetative hybridization.

[30] Charles M. Rick, "The Grafting Relations of Wilty Dwarf, a New Tomato Mutant," *American Naturalist*, 1952, *86:* 173-184.

[31] Lysenko (n. 24-25).

[32] Hans Stubbe, Über die vegetative Hybridisierung von Pflanzen Versuche an Tomatenmutanten," *Kulturpflanze*, 1954. *2:* 183-236. [Quotation appears on pp. 235-236 and is emphasized.]

[33] *Ibid.*, p. 236. [It is particularly noteworthy that Stubbe's careful and extensive investigations were being carried out during the height of Lysenko's influence in the Institute for Genetics at Martin-Luther-Universität in Halle-Wittenberg, D.D.R. The final sentence of the paper, which directly follows the passage cited by Blacher is very precise in its thrust: "Die Angaben sowjetischer Autoren konnten daher nicht bestätigt werden."]

[34] Daniil Vladimirovich Lebedev, "Novye dannye k voprosu o vegetativnoi gibridizatsii" ["New Data on the Question of Vegetative Hybridization"], *Bot. Zhurn.* [*Journal of Botany*], 1955, *40:* 603-604.

[35] Nikolai Vasilievich Tsitsin and M.Z. Nazarova, "Opyty po otdalennoi vegetativnoi gibridizatsii rastenii" ["Experiments in Remote Vegetative Hybridization in Plants"], *Izv. AN SSSR, seria biol.* [*News of the Academy of Sciences of the USSR, Biology Series*], 1953, *no. 1:* 20-36.

According to H. Böhme's data, directed changes do not occur in grafted plants, grafts do not affect the segregation of hybrid traits, and surely they do not produce anything resembling a vegetative hybrid.[36] Similarly, the experiments of Anton Romanovich Zhebrak, which were grafts between pure lines of peas possessing contrasting traits, did not lead to directed changes, much less to the formation of vegetative hybrids.[37]

In the same year as the appearance of Zhebrak's work V. Gaevskii reported on unsuccessful attempts to obtain vegetative hybrids at experimental stations in Poland.[38] A year later L. Rzegovinska briefly described the results of experiments in which she performed 2126 grafts among three species of lupine—white, yellow, and narrow-leaved. All of these experiments likewise failed to produce vegetative hybrids.[39]

Attempts by Czechoslovakian investigators to reproduce the results of vegetative hybrids that Lysenko and Glushchenko had described were just as unsuccessful.[40]

I.F. Liashchenko grafted albino sunflower plants onto green stocks and obtained a greening of the scion in a number of cases. From the seeds of twenty-five plants, 350 seedlings were grown. The latter were all albino, that is, the greening of the albino scions under the influence of the green stock turned out to be nonheritable.[41]

In 1959 Glushchenko gave a report at the International Colloquium on Transplantation held in honor of the 100th anniversary of Daniel's birth.[42] Besides reviewing works of Soviet investigators, he included data gleaned from the foreign press through which he intended to show the objectivity and importance of accounts of vegetative hybrids. In a review article

[36] H. Böhme, "Untersuchungen zum Problem der genetischen Bedeutung von Propfungent zwischen genotypisch verschiedenen Pflanzen," *Z. Pflanzenzucht,* 1954, *33:* 367–418; "Weitere Untersuchungen zum Problem der genetischen Bedeutung von Pfropfungen zwischen genotypisch verschiedenen Pflanzen," *ibid.,* 1597, *38:* 37–50.

[37] Anton Romanovich Zhebrak, "Vliianie privivki na razvitie nasledstvennykh priznakov u gorokha" ["The Effect of Grafting on the Development of Hereditary Traits in Peas"], *Dokl. AN SSSR* [*Papers of the Academy of Sciences of the USSR*], 1956, *106:* 1099–1120; "Vliianie privivki na semennoe potomstvo i na rasshcheplenie gibridov vo vtorom pokolenii" ["The Effect of Grafting on Seed Offspring and the Breakdown of Hybrids in the Second Generation"], *ibid.,* 1956, *107:* 325–327

[38] V. Gaevskii, in *Problemy botaniki* [*Problems of Botany*], 1956, *12:* 698–705.

[39] L. Rzegocińska, "Attempts at Generative Hybridization of Different Species of Lupine by Vegetative Grafting," *Bull. Acad. polon. sci. sér. biol.,* 1957, *no. 5/6:* 183–186.

[40] A. Haspelová, L. Rabanová, "Discusia o stave genetiky v ČSR" ["Discussion of the State of Genetics in the Czechoslovakian Soviet Republic"] *Biologia,* 1954, *12:* 310–313.

[41] I.F. Liashchenko, "K voprosu o vegetativnoi gibridizatsii u podsolnechnika (Helianthus annuus)" ["On the Question of Vegetative Hybridization in Sunflowers (Helianthus annuus)"], *Bot. zhurn.* [*Journal of Botany*], 1958, *43:* 710–712.

[42] Ivan Evdokimovich Glushchenko, "Lucien Daniel et l'état actuel du probléme de l'hybridation végétative des plantes et des animaux," *Bull Soc. sci. Bretagne,* 1959, *34:* 253–277.

D.S. Dean evaluated the examples used in Glushchenko's report and discussed the concept of vegetative hybridization in general.[43] In order to prove the possibility of vegetative hybridization, Dean felt it was necessary to show that the characteristics which changed as a result of the grafting were transmitted by means of sexual propagation. The transmission of such changes to the first sexually produced generation alone did not, however, constitute sufficient evidence for vegetative hybridization because it was entirely possible that genetic materials of the chimeric mother could influence the phenotype of this first generation. Since these materials could not be self-replicated, their influence could not be viewed as hybridization in the generally accepted sense of the word. As Doncho Kostoff's work showed, the stock could have an effect on the phenotype of the scion also in rare cases when it disrupted the chromosomal balance or, as Ray Harland Roberts suggested, when it caused a mutation.[44,45] Dean believed that in evaluating the possibility of vegetative hybridization, one should exclude phenomena of DNA transduction and the influence of viruses. The latter only simulate those changes which might be mistaken for the results of vegetative hybridization.

[In the same anniversary report] Glushchenko referred to the work of J.L. Fennel, who had studied sexual hybridization in grapes and had used grafting as a means of obtaining pollen at the appropriate time for cross-fertilization.[46] Despite the unambiguous nature of Fennel's statements, Glushchenko spoke of his work as if it confirmed the phenomenon of vegetative hybridization. Glushchenko also inappropriately cited the work of Doncho Kostov and M. Stoilov as an example of vegetative hybridization.[47] These researchers had grafted cucumbers onto melons and their work dealt only with the effects revealed during the year the grafts had been done. Glushchenko also failed to mention that the stock was homozygous and that the control grafting of cucumber to cucumber caused changes similar to those obtained in the experiment. Glushchenko's citation of the work of Cl.-Ch. Mathon and M. Stroun was irrelevant for his survey.[48] These workers had grafted the embryo of one cereal onto the endosperm of another, and in their opinion the results did not serve as

[43] D.S. Dean, "An Evaluation of the Claims of I.E. Glouchtchenko for Vegetative Hybridisation in Plants," *J. Hered.,* 1962, *53:* 215–221.

[44] Doncho Kostov, "Chromosomal Aberrants and Gene Mutation in Nicotiana obtained by Grafting," *J. Genet.,* 1930, *22:* 399–418.

[45] R.H. Roberts, "Theoretical Aspects of Graftage," *Bot. Rev.,* 1949, *15:* 423–463.

[46] J.L. Fennel, "Timing and Production of Grape Pollet by Grafting," *J. Hered.,* 1945, *36:* 183–86.

[47] Doncho Kostov and M. Stoilov, "Grafting Experiments of Cucumber upon Squash," *Compt. Rend. Acad. Bulgare Sci.,* 1948, *1:* 49–52.

[48] Cl.-Ch. Mathon and M. Stroun, "Quelques aspects de l'hybridation végétative des Céréales," *Compt. Rend. Acad. Sci. Paris,* 1955, *241:* 322–328.

evidence of the transmission of the recipient's traits to the plants which grew from the grafted embryos. The survey also included a work by M. Pichenot who had transplanted *Solanum sisymbrifolium* onto *Datura stramonium.*[49] Glushchenko considered this graft as an example of the production of a vegetative hybrid as well as "an improved variety preserved in sexual propogation." In fact, the characters which Pichenot obtained by grafting were not the characters of the stock. Glushchenko drew the same type of unfounded conclusions from another work in which Pichenot had grafted a petunia onto a jimsonweed.[50] Concerning experiments on tomatoes by I. Kazahara and associates, Glushchenko wrote that they were "crowned with success," that is, that true vegetative hybrids had been produced.[51] These experiments, however, were invalid because the stock was not homozygous for genes determining coloration or fruit-shape.

Comparing the phenomena described in the above works and others mentioned in Glushchenko's survey, Dean found that they were too varied and did not allow for a unified or unambiguous explanation, let alone an explanation in terms of vegetative hybridization. In Dean's opinion, only the work of R. Glavinich satisfied the minimal requirements for experiments presuming to prove the possibility of vegetative hybridization. He considered it likely, however, that Glavinich's results might be explained as well by standard genetic principles. Glavinich's book appeared in Russian with an introduction by Glushchenko.[52] The introduction covered a selective sampling from the literature of those data which confirmed the possibility of vegetative hybridization and failed to mention works which contained criticism of these data or reported experiments with negative results. Glushchenko merely remarked that vegetative hybridization had for a number of years been the subject of a heated debate. An article by Donald Michie, "The Third Stage of Genetics," in the collection *A Century of Darwin* also made reference to the work of Glavinich.[53] The author noted that Glavinich's interpretation of her results in a paper presented at the Hague was extremely forced. In it she had reported the segregation of the traits of leaf shape and coloration of fruits in the sexual reproduction of the

[49] M. Pichenot, "Essai de greffage de Solanum sisymbrifolium Lamck, sur Datura stramonium L.," *Compt. Rend. Acad. Sci. Paris,* 1956, *243,* no. 25: 2137-2139.

[50] M. Pichenot, "Modifications apportées par le greffage dans le développement du Petunia violacea Lindl," *Compt. Rend. Acad. Sci. Paris,* 1957, *244:* 1669-1671.

[51] J. Kazakara, T. Nakamura, and I. Yoneama, "Vegetativnaia gibridizatsiia tomatov" ["Vegetative Hybridization of Tomatoes"], *J. Fac. Agric. Iwate Univ.,* 1955, *2:* 149-160 (in Japanese with a summary in Russian).

[52] R. Glavinich, *Izmenenie nasledstvennosti rastenii putem privivki* [*Alteration in Heredity of Plants Through Grafting*], trans. from Serbian by Z. Eshich, ed. and foreword by I.E. Glushchenko, academician of the All-Union Lenin Academy of Agricultural Sciences (Moscow: 1959).

[53] Donald Michie, "The Third Stage of Genetics," in *A Century of Darwin,* ed. S.A. Barnett (Cambridge, Mass.: Harvard University Press, 1958), pp. 56-84.

tomato variety "Golden Trophy" which had been grafted onto the "potato leaf" variety. According to Michie, one might think of an analogy with transduction by a phage; however, such a mechanism of inheritance invoked to explain the wandering of chromosome fragments in higher plants was absolutely unthinkable. In any case, the data reported by Glavinich stand in irreconcilable contradiction to the results of the meticulously conducted experiments of Stubbe, Böhme, Kraevoi, and many others.

The large body of experimental material of Kraevoi, published in part from 1941 to 1958, was examined in greater detail in a book already cited [see fn. 9]. Kraevoi described data for reciprocal grafts of different varieties of potatoes which listed the characteristics of successive tuberous generations. Over the course of five years he had performed numerous grafts between wild and cultivated potatoes; grafts among tomatoes with various colorations and leaf and fruit forms; grafts of tomato to thornrose and vice versa, including repeated grafts; grafts of tomato onto tobacco and vice versa, including repeated grafts; grafts between different varieties of tobacco; and grafts between radishes to cabbages. In all cases where the fertility of the experimental material permitted, Kraevoi checked the inheritance of acquired changes in one or two seed generations, invariably with negative results. He carried out all these numerous and varied experiments according to the basic rules of experimental work, that is, with provision for appropriate controls. His experiments proved without a doubt that the assertions of Lysenko, Glushchenko, and their successors concerning the production of true vegetative hybrids were based not on irreproachable factual material but on *a priori* assumptions of the inheritance of acquired characters.

We should pay special attention to those studies where the results were sometimes interpreted as proof of vegetative hybridization in animals. Results of four categories of experiments were thus interpreted; 1) intervarietal ovary, testicle, and fertilized-egg transplants; 2) partial intervarietal and even interspecies exchanges of egg albumen; 3) temporary parabiotic crosses; and 4) transfusions of foreign blood. The results of the first two categories in fact bear no relation to the question of vegetative hybridization in animals (see chapters 15 and 18).

To answer questions concerning inheritance, G.V. Boriachok-Nizhnik and M. Gashek carried out parabiotic experiments on young rabbits and on bird embryos, respectively.[54,55] A surgical joining of pairs of female rabbits for approximately a month did not in most cases have any particular effect

[54] G.V. Boriachok-Nizhnik, "Opyty vegetativnoi gibridizatsii zhivotnykh" ["Experiments in Vegetative Hybridization of Animals"], *Zhurn. obschchei biol.* [*Journal of General Biology*], 1952, *12:* 233-251.

[55] M. Gashek, "Voprocy vegetativnoi gibridizatsii i peresadki tkanei u teplokrovnykh zhivotnykh" ["Questions of Hybridization and Tissue Transplant in Mammals"], *Zhurn. obshchei biol.* [*Journal of General Biology*], 1955, *16:* 405-412.

on the offspring. Only one experiment produced results which Boriachok-Nizhnik interpreted as evidence of vegetative hybridization. Here young females of the angora (white) and Flanders (black) varieties were joined together for thirty-six days. After separation and pairing with a white angora male, the experimental angora female gave birth to seven white rabbits, six short-haired and one long-haired. The dominant parabiotic partner had no influence on the coloration of its partner's offspring. The trait of hair length could not serve as evidence of vegetative hybridization since the cub rabbits showed a segregation of the hair length trait in further pairings among themselves, that is, they were heterozygous. Moreover, in this work, as in all similar works, the investigator made crosses without taking into consideration the requirements for rigorous genetic experiments.

Gashek's work had even less significance for the idea of vegetative hybridization in animals. Gashek united in pairs the embryos of different varieties of chickens; he also joined the embryos of chickens to those of ducks, turkeys, pheasants, and guinea fowl. In the overwhelming majority of cases there was no effect whatsoever of one parabiotic partner on the other. Only in one experiment did a hen, which had developed from a White Leghorn embryo that previously had developed in parabiosis with a Rhode Island embryo, yield more darkly colored chicks than a White Leghorn control when both were mated to a Rhode Island rooster. It is not known why this hen was not paired with a rooster of her own variety; the influence of the parabiosis, if it had occurred, would then have been perfectly clear. But from Gashek's random and numerically insufficient data it is impossible to come to a conclusion concerning the possibility of vegetative hybridization.

Experiments with the transfusion of foreign blood, intended to alter hereditary traits of the offspring, were significantly more numerous. The findings of these experiments were published in professional journals and read at international symposia and conference.[56]

[56] Khila Faivilovich Kushner, "Vliianie metabolicheskikh faktorov na nasledstvennost' zhivotnykh," *Agrobiol.*, [*Agrobiology*], 1957, *no. 1:* 19-35 (H.F. Kushner, "The Influence of Metabolic Factors on the Heredity of Animals," *Proc. Intern. Genetic Symposia,* Tokyo and Kyoto: 1957); Kh. F. Kushner, "Nasledovanie ismenenii v okraske opereniia u kur, podvergnutykh perelivaniiu chuzherodnoi krovi," *Zhurn. obshchei biol.,* 1958, *19:* 357-368 (Kh. F. Kushner, "Inheritance of Changes in Feathering Pigmentation in Fowls (Hens) Subjected to Foreign Blood Transfusion," *'Proc. X Intern. Congr. Genet.,* 1958, *2;* J.M. Stroun, L.R. Stroun-Guttiere, J. Rossi, and M. Stroun, "Modifications de la poule Leghorn traitée par le sang de pintade," *Proc. X Intern. Congr. Genet.,* 1958, *2;* P.M. Sopikov, "The Alteration of Certain Properties and Characters in Fowls by Means of Parental Transfusion of Blood and their Fixation in the Offspring," *Mem. XI Congr. Mund. Avic.* (Mexico: 1958), pp. 109-116; P.M. Sopikov, "Izmenenie nasledstvennosti u zhivotnykh posredstvom perelivaniia krovi, transplantatsii tkanei i nasledovanie priobretennykh priznakov i svoistv" ["Change in the

After the publication in 1871 of negative results of experiments by Francis Galton (see chapter 4) who had carried out intervarietal blood transfusions among rabbits, P.M. Sopikov was the first to reestablish the use of this method for affecting hereditary traits.[57] He gave young White Leghorn chickens 5 ml transfusions of blood twice a week either from roosters of the Australorp variety (black) or from turkeys or geese. Sopikov himself and Kushner, who cited Sopikov's data, asserted that in the fourth generation, given continued blood transfusions in previous generations, a certain number of individuals with black plumage like that of the Australorp variety appeared from pairings with Leghorn roosters.[58] The appearance of colored feathers was also described in a portion of the offspring of the white chickens who received blood transfusions from geese and turkeys. K Bratanov subsequently confirmed the latter observation.[59] A.M. Gromov and P.I. Feoktistov[60] A.M. Gromov,[61] and E.E. Pen'onzhkevich and G.A. Mishin[62] gave chickens blood transfusions from chickens of other varieties, from turkeys, and from pheasants, and they all described changes in plumage coloration in a portion of the offspring. Kushner carried out experiments with blood transfusions from New Hampshire hens and wild ducks to hens and roosters of the Leghorn variety. He obtained a change in coloration in a portion of offspring of the experimental hens, but it would be impossible to draw any definite conclusions from his data. Somewhat later Pierre Leroy reported experiments with blood transfusions from pheasants to Rhode Island chickens. In these experiments a change in plumage coloration appeared in a portion of the offspring.[63] A year later

Heredity of Animals Through Blood Transfusion, Tissue Transplantation, and the Inheritance of Acquired Traits and Characters"], in the collection *Nasledstvennost' i izmenchivost' zhivotnykh, rastenii i mikroorganizmov* [*Heredity and Variability in Plants, Animals, and Microorganisms*], 1959, *1:* 554-560.

[57] P.M. Sopikov, "Izmenenie nasledstvennosti putem parenteral'nogo vvedeniia krovi" ["Alteration of Heredity Through Parenteral Injection of Blood"], *Agrobiol.* [*Agrobiology*], 1954, *no. 6:* 34-45.

[58] Kushner (n. 56, 1957).

[59] K. Bratanov, Vegetativnaia gibridizatiia ptits" ["Vegetative Hybridization in Fowl"] *Izv. AN SSSR, seriia biol.* [*News of the Academy of Sciences of the USSR, Biology Series*], 1954, *no. 1:* 53-58.

[60] A.M. Gromov and P.I. Feoktistov, "Izmenenie nasledstvennosti u kur posredstvom perelivaniia krovi" ["Alteration of Heredity in Chickens Through Blood Transfusion"], *Ptitsevodstvo* [*Poultry Breeding*], 1956, *no. 6:* 42-45.

[61] A.M. Gromov, "Izmeneniia u kur, voznikaiushchie pod vliianiem perelivaniia chuzherodnoi krovi" ["Variations Arising in Chickens Under the Influence of Transfusions of Foreign Blood"], *Ptitsevodstvo* [*Poultry Breeding*], 1959, *no. 9:* 26-27.

[62] E.E. Pen'onzhkevich and G.A. Mishin, "Izmenenie nasledstvennosti u belykh leggornov v rezul'tate in'ektsii im krovi serykh tsesarok" ["Alteration of Heredity of White Leghorns Through Blood Transfusions from Grey Guinea-fowl"], *Ptitsevodstvo* [*Poultry Breeding*], 1959, *no. 8:* 32-33.

[63] Pierre Leroy, "Observations faits sur les poules 'Rhode Island Red' génétiquement

(*contd.*)

the same author published a survey article in which he posed these questions: "To what should changes observed following blood transfusions be ascribed? Should mutagenic factors be considered? The action of a special enzymatic factor? The action of a virus, as suggested by André Lwoff and Ph. L'Héritier? Is there a direct effect of nucleic acids present in excess in the blood of a fowl, or of a protein complex with a nucleic acid, that induces the formation of a new genetic structure? Does a relationship arise between genetic inhibitors (in the sense of François Jacob and Jacques Monod) and individual cell components? We don't know."[64]

The hypothetical role of the DNA in blood transfusions is based on data of Jacques Benoit and co-authors. These investigators reported a successful induction of hereditary changes of beak coloration in Peking ducks by DNA from ducks of the Khaki-Campbell variety.[65] E. Wolff responded to these results with an article which evaluated them as an important discovery showing the way to produce "directed mutations."[66]

Benoit's results were evaluated quite differently by M. Aloisi, professor at Müden University, and by Jean Rostand, a member of the Paris Academy of Sciences. Aliosi wrote in a letter published in the journal *Rinashita* that the question touched upon by Benoit "from a purely scientific point of view has nothing to do with the hereditary transfer of acquired characteristics. . . . Even if the French experiments were proven correct (however, they have little plausibility and authoritative doubts have already been expressed concerning their veracity), they would only confirm in paradoxical fashion the significance of Weismann's germ-plasm."[67] Rostand expressed the same thought. "It has been said . . . that the experiment with ducklings finally proves this phenomenon [the existence of the inheritance of acquired characters.] . . . There is nothing more mistaken than such an assertion. . . . Actually, there is nothing in common between a directed mutation—that is to say an alteration of a gene induced directly by DNA—and the transfer of an acquired trait."[68] The results obtained by

contrôlées et sur leurs descendants de 1 et 2 générations après injections répétées de sang de pintade," *Compt. Rend. Acad. Sci. Paris*, 1962, *254:* 756–758.

[64] Leroy, "'L'hybridation végétative' chez les oiseaux," *L'Annee biol.*, 1963, Ser. 4, 2: 337–370.

[65] J. Benoit, P. Leroy, Colette Vendrely, and Roger Vendrely, "Des mutations somatiques dirigées sont-elles possibles chez les oiseaux?" *Compt. Rend. Acad. Sci. Paris*, 1957, *244:* 2320–2321.

[66] E. Wolff, "A propos d'une decouverte récente en biologie. Les 'mustations dirigees' chez le canards," *Rev. Philos.*, 1958, *148:* 14–23.

[67] M. Aloisi, letter in *Rinascita*, 1957, *no. 9:* 483.

[68] Jean Rostand, "Connaisson-nous la base chemique de l'hérédité," *La Revue de Paris*, Sept. 1957, pp. 26–32. [Quotation appears on p. 31.] Citations of Aloisi and Rostand are given according to a leading editorial article, "O nekotorykh problemakh sovetskoi biologii (po povodu stat'i T.D. Lysenko 'Za materializm v biologii')" ["Concerning Certain Problems of

Benoit obviously depended on some flaw in the experiment. Soon afterwards J. Svoboda and V. Hašková published a work in which they reported negative results in an attempt to induce hereditary changes in ducks through the injection of DNA from one variety into another.[69] Similarly, negative results were obtained by Thomas L. Perry and D. Walker[70] and by J.G. Bearn and K.S. Kirby[71] on rats, by Boris L. Astaurov and co-authors on the mulberry silkworm,[72] by R.E. Burger and co-authors on rats,[73] and by others. If the results of the transfusion of whole blood might nevertheless be attributed to the DNA of the nuclei of red corpuscles, they still fail to explain the experiments in which an analogous action was claimed for the plasma of foreign blood. For example, following the transfusion of blood plasma from New Hampshire, Rhode island, and Australorp chickens and from turkeys to White Leghorns, the same changes in the offspring of experimental chickens appeared that had appeared with the transfusion of whole blood.[74]

Besides publications that confirmed the changes of characters in offspring after the injection of foreign blood, there were reports of investigations that yielded definitely negative results. The detailed work of J.L. Kosin and M. Kato belongs to the latter group.[75] Here it is reported that

Soviet biology (in Relation to T.D. Lysenko's Article 'In Defense of Materialism in Biology')"], *Bot. zhurn.* [*Journal of Botany*], 1958, *43:* 1142.

[69] J. Svoboda and V. Hašková, "Failure to Produce Somatic Changes Between Strains of Ducks by Means of Specific DNA," *Folia biol.* (Prague), 1959, *5:* 402–404.

[70] Thomas L. Perry and Dorothy Walker, "Failure of Deoxyribonucleic Acid to Effect Somatic Transformation in the Rat," *Proc. Soc. Exper. Biol.*, 1958, *99:* 717–720.

[71] J.G. Bearn and K.S. Kirby, "Failure of Deoxyribonucleic Acid to Produce Pigment Changes in the Albino Rat," *Exper. Cell. Res.*, 1959, *17:* 547–549.

[72] Boris Lvovich Astaurov, T.A. Bedniakova, G.I. Gintsburg, I.B. Zbarskii, and G.R. Ramenskaia, "Popytka polucheniia nasledstvennykh izmenenii u tutovogo shelkopriada Bombyx mori posredstvom mezhlineinykh in''ektsii desoksiribonukleinovoi kisloty" ["An Attempt to Obtain Heredity Alterations in the Silkworm, Bombyx mori, by Means of Injections of DNA), *Dokl. AN SSSR* [*Papers of the Academy of Science of the USSR*], 1960, *134:* 449–452.

[73] R.E. Burger, R.N. Shoffner, and C.W. Roberts, "Treatment of Fowl Sperm and Developing Embryos with Deoxyribonucleic Acid Extracts," *Poultry Sci.*, 1961, *40:* 559–564.

[74] Khila Faivilovich Kushner, E.V. Tolokonnikova, and I.G. Moiseeva, "Izmenenie okraski opereniia u potomstva kur v rezul'tate vlivaniia im razlichnykh komponentov chuzherodnoi krovi" ["Alteration of Plumage Coloration in the Offspring of Chickens as a Result of the Transfusion of Various Foreign Blood Components"], *Dokl. AN SSSR* [*Papers of the Academy of Sciences of the USSR*], 1959, *129:* 674–677; E.V. Tolokonnikova, I.G. Moiseeva, and S.A. Bogatyreva, "Izmenenie okraski opereniia kur v rezul'tate vvedeniia im razlichnykh komponentov chuzherodnoi krovi" ["Alteration of Plumage Coloration in Chickens as a Result of Transfusion of Various Foreign Blood Components], *Zhurn. obshchei biol.* [*Journal of General Biology*], 1961, *21:* 66–73.

[75] J.L. Kosin and M. Kato, "A Failure to Induce Heritable Changes in Four Generations of the White Leghorn Chicken by Inter- and Intraspecific Blood Transfusion," *Genet. Res.*, 1963, *4:* 221–239.

starting at the age of two to five days old chicks of the Washington variety of the White Leghorn breed received blood transfusions every four days from New Hampshire chicks or from Bronze turkey chicks. More than three hundred offspring were studied in three successive generations, during which plumage coloration, body weight, egg shell coloration, fertility, and hatching rate were recorded. The blood plasma and muscle tissue were subjected to immunologic, chromatographic and electrophoretic analysis. The investigators detected no shift in the direction of the donor's traits on the basis of any of these criteria. A Buschinelli likewise obtained negative results in an experiment in which blood of the South American fowl *Crax fasciolata* was transfused into two White Leghorns. Over the course of three generations he discovered no effect on hereditary traits.[76]

Regarding these transfusion experiments, it is important to note, as did Leroy in his survey, that not one of the experiments obtained phenotypic changes in the animals which received the transfusions. In order to observe changes which were transmitted to succeeding generations, the experimenters had to wait for the offspring of the first generation.[77] In other words, in blood transfusion experiments somatic induction was not detected; the inheritance of acquired traits in the strict sense of the word was not found.

The experiments of Astaurov and Vera P. Ostriakov-Varshaver, which were outstanding in design and execution, were decisive in denying the possibility of vegetative hybridization and somatic induction in general.[78] These appeared in print earlier than many of the articles which attempted to prove the existence of vegetative hybridization but were ignored by the authors of such articles.

In their experiments Astaurov and Ostriakov-Varshaver obtained androgenous hybrids of two varieties of silkworm. They heated to 40°C the eggs of the wild *Bombyx* (*Theophilia*) *mandarina* at the second cleavage stage. This led to the destruction of mitotic spindles and prevented the nuclear material of the egg from further development. They then fertilized these eggs with spermatazoids of the domesticated *Bombyx mori,* a variety possessing a number of traits recessive to their counterparts in the wild variety. Because of natural polyspermy (usually only one male pronucleus combines with the female) and because of the deactivation of

[76] A. Buschinelli, "Injeçoes periodicas de sangue em aves o suas implicaçoes geneticas," Tese. Univ. de São Paulo (Brazil: 1961). Cited according to Kosin and Kato (n. 75).

[77] Leroy (n. 64), p. 344.

[78] Boris L'vovich Astaurov and Vera Petrovna Ostriakova-Varshaver, "Poluchenie polnogo geterospermnogo androgeneza u mezhvidovykh gibridov shelkovichnogo chervia (Eksperimental'nyi analiz sootnositel'noi roli iadra i tsitoplazmy v razvitii i nasledstvennosti)" ["Production of a Fully Heterospermic Androgen in Interspecies Hybrids of Silkworms (An Experimental Analysis of the Interrelationship of the Roles of Nucleus and Cytoplasm in Development and Heredity)"], *Izv. AN SSSR, seriia biol.* [*News of the Academy of Sciences of the USSR, Biology Series*], 1957, *no. 2:* 154–175.

the female nucleus, two male nuclei often fused within one egg. The experimental eggs nevertheless proceeded to develop. From the eggs arose caterpillars, crysalises, and moths (only males because of the absence of an X-chromosome) that possessed all their father's traits and completely lacked their mother's. From these experiments Astaurov and Ostriakova-Varshaver drew the direct conclusion that the material determinants of heredity are located in the nucleus and not in the cytoplasm—confirming incidentally what Austaurov had concluded in an earlier article. At the same time they enlisted these data for the discussion of other general issues in biology, in particular the question of vegetative hybridization in animals and somatic induction. "The question of vegetative hybridization in animals," Astaurov and Ostriakova-Varshaver wrote, "resurrects under a new and highly unsatisfactory term, the long since rejected issue of somatic induction, which, in its turn, is part of the more general problem of the inheritance of favorable, acquired characteristics."[79]

Having cited various experiments (discussed in this book in chapters 14, 16, 18, and 19) that presumed to prove the specific influence of various operations on the offspring—e.g., parabiotic fusion, exchange of a portion of the albumin between birds' eggs, transfusion of foreign blood, intervarietal transplants of ovaries and testicles, and transplantation of foreign-fertilized ovicells—and having expressed reasonable doubt as to the validity of changes described in the reports, Astaurov and Ostriakov-Varshaver noted that the essential question posed in these works was answered unequivocally by their own recent experiments. "In the experiments on intervarietal androgeny . . . ," they wrote, "we have an extremely profound case . . . the restructuring of the egg system (nucleus and oviplasm) whereby the entire cytoplasm and reserve nutrient substances, which exceed the mass of the nuclear material by many thousands of times, are replaced by the cytoplasm of another variety. Despite the fact that the foreign material has the opportunity to act on the traits of the developing individual over the course of its entire ontogenesis, this not only does not change the hereditary traits of subsequent generations, but it does not even effect the traits of the 'vegetative hybrid' itself, which instead correspond exactly to the genotype contributed by the nucleus. In light of these facts it would be simply naive to believe that directed changes in the hereditary traits can be achieved through the injection of several cubic centimeters of foreign blood or the partial exchange of the stores of albumin nutrients."[80]

[79] Boris L'vovich Astaurov, "Znachenie opytov po merogonii i androgenezu dlia teorii razvitiia i nasledstvennosti" ["The Significance of Experiments with Meregony and Androgeny for a Theory of Development and Heredity"], *Usp. sovrem. biol.* [*Successes of Contemporary Biology*], 1948, *25:* 49–88.

[80] Astaurov and Ostriakova-Varshaver (n. 78), p. 172.

CHAPTER 20

Conclusion

The main cause of the lively discussion over the issue of the inheritance of acquired characters was the fact that that question became tied, especially in the second half of the nineteenth century, to the controversy concerning the mechanisms of evolution. Two schools of evolutionary thought arose, which were distinguished by the following basic differences. According to one, following the lead of Lamarck, evolution was regarded as a phenomenon of direct adaptation. Proponents believed that hereditary changes corresponding to conditions of the environment arose under the direct influence of factors in that environment or of use or disuse of organs. The other school, founded by Darwin, proceeded from the idea that hereditary change was not directed. According to this, of the great variety of forms that arose, the ones selected during the struggle for survival were those whose traits satisfied the conditions of existence.

The dearth of information on the source of hereditary variations, on the mechanism of their origin, and on the laws of inheritance, as well as the lack of rigorous experiments by which one could confidently judge whether acquired traits were inherited, led Darwin to accept the existence of both paths for evolution. Along with evolution by natural selection Darwin admitted the possibility of evolutionary change through direct adaptation. He felt obliged, however, to reckon with the corollaries that necessarily followed from this assumption. Referring to examples which could be interpreted as inheritance of functional changes, he asked the question, how could the use or disuse of some body part remote from the sex glands affect sex cells so that progeny would inherit the changed traits? One should either admit that changed organs could not possibly have a directed influence on sex cells, or else one must construct a hypothetical explanation for such an influence.

At that time, belief in the inheritance of acquired characters was almost universal. As Gavin de Beer noted, "Before the 19th century the people who rejected the inheritance of acquired traits could be counted on the fingers of one hand."[1] Almost the same situation prevailed in the middle of the nineteenth century. Darwin succumbed to the spell of the widely

[1] Gavin de Beer, *Charles Darwin: Evolution by Natural Selection* (London: 1963), p. 164.

held view and offered his pangenesis hypothesis. He himself later spoke of this in very unflattering terms, calling it "garbage" and "frivolous nonsense," and yet he did not want to part with it since he could find nothing [satisfactory] with which to replace it.

The idea of pangenesis goes back to Hippocrates. Analogous views were expressed before Darwin by Ray, Buffon, and Maupertuis, and after Darwin by Erlsberg and Haeckel. Consistent Darwinism, strictly speaking, has no need to assume the inheritance of acquired traits. Haeckel did not understand this, so he placed in the category of inheritance of acquired variations cases which Darwin himself had discussed very cautiously, and he added his own unfortunate examples. Haeckel even looked sympathetically upon psycho-Lamarckian views of his pupil Richard Semon. Semon equated inheritance with memory, and in this respect he followed in the footsteps of Hering, Butler and Haeckel himself, who wrote about the perceptions and memory of plastidules (hypothetical self-replicating protein molecules).

A new historical stage was reached when Weismann presented the idea that the problem of inheritance of acquired traits could not be resolved by a simple accumulation of non-contradicting examples, that clarification of the truth required argumentation by precise experiments. The legitimacy of this demand was quite obvious to biologists who were convinced of the usefulness of employing the experimental method in the study of phenomena of life, namely, physiologists, embryologists, and geneticists. But the physiologist and the embryologist dealt only with a given individual organism and were not interested in the effect of an experimental factor over successive generations. Only the geneticist, by the very nature of his subject, could justifiably speak of the possibility of a transfer to progeny of changes experimentally induced in the parents. Experiments which demonstrated the nonheritability of acquired characters were, as a rule, conducted by geneticists or by investigators who knew the experimental methods of genetics.

Biologists of other specialties—paleontologists, systematists, biogeographers, ecologists—who by the very nature of their subject rarely had the opportunity to employ the experimental method, nevertheless often felt it possible, by supporting themselves with indirect evidence, to speak out on the inheritance of acquired characters. We examined in chapter six the views of paleontologists, who had less basis than specialists in any other field of biology to assert the inheritance of acquired traits. Here we will briefly mention the views of investigators in the other fields of biology just listed. The majority of them were botanists, and some even favored manipulative experimental work, but as a rule they dealt not with genetic but with ecological or biogeographical experiments.

Such experiments consisted of transplanting a plant from one geo-

graphical or ecological environment to another and observing the changes that resulted, which sometimes had an adaptive character. The results of such research were analyzed in detail by Georg Klebs and Kliment A. Timiriazev. Klebs described the views of Richard von Wettstein, a Lamarckian who defended the idea of "functional adaptation." In this view, "a causal significance is attributed to function," but as Klebs pointed out, "this assertion is not only unfounded, it even lacks necessary clarity."[2] Wettstein believed that in order to explain the mechanism of evolution one must proceed from a compromise between Lamarckian and Darwinian concepts. In the plant world, he felt that by far the greater role is played not by natural selection, but by direct adaptation, "the adaptive ability of the individual to undergo changes and also the ability of the organism to inherit features acquired in this manner."[3] Wettstein, however, could supply only indirect evidence for his assumption.

Timiriazev fully agreed with Kleb's assessment of the views of "Wettstein, Warming, and other contemporary writers, who endow this expression [functional adaptation] with the quite unscientific meaning of some inexplicable, direct, goal-directed environmental influence."[4] Whereas Wettstein simply asserted that plants directly adapt to their environment and did not analyze the possible mechanism, Warming "proposed that plants possess a special inherent power or ability to adapt themselves directly to new conditions, i.e. to vary . . . in a direction conducive to life." "This concept is purely teleological," Klebs concluded.[5]

Timiriazev also disputed the views of Julien N. Constantin and George Henslow, who thought that a conclusion in favor of the inheritance of acquired traits "can be made on the basis of simple observation, and if that method is not so rigorous, it is still convincing because of the abundance of facts that suggest such inheritance."[6]

Henslow used such argumentation in his treatises "The Origin of Plant Structures by Self-adaptation to the Environment" and "*The Heredity of the Acquired Characters in Plants.*"[7] In his opinion, plants living in

[2] Georg A. Klebs, *Proizvol'noe izmenenie rastitel'nykh form Wilkürlich Entwickelungsänderungen bei pflanzen,* trans. K.A. Timiriazev, *Soch.* [*Works*], 1939, *6:* 357. [For further details see chapter 10, n. 21.]

[3] Richard von Wettstein, "Der Neo Lamarckismus und seine Beziehung zum Darwinismus," *Verh. d. Gesell. d. deutscher Naturforsch. u. Arzte. 74th Versammlung z Karlsbad, 21-27 Sept. 1902, pt. 1,* p. 88. [Passage is emphasized in original.]

[4] Timiriazev (n. 2), p. 359.

[5] Klebs (n. 2), pp. 436-437.

[6] K.A. Timiriazev, "Istoricheskii metod v biologii" ["The Historical Method in Biology"], in *Soch.* [*Works*], vol. VI, p. 181.

[7] George Henslow, "The Origin of Plant-structures by Self-adaptation to the Environment. Exemplified by Desert or Xerophilous Plants," *J. Linnean Soc. Bot.,* 1895, *30:* 218-63, rev. in *Bot. Chl.,* 1895, *61:* 315-318; George Henslow, *The Heredity of Acquired Characters*

different places but under the same conditions resembled one another because of the direct result of external influences. Henslow tried to confirm this conclusion with experiments that demonstrated the influence of identical conditions on plants. He proposed that variations which arose during these experiments, especially if the influence were sufficiently prolonged, would become fixed in the progeny. Henslow's results were unconvincing, but his conclusions clearly contradicted the old data of Alexis Jordan and especially the unambiguous results of Nägeli's experiments (see chapter 7).

With characteristic incisiveness, Timiriazev examined Henslow's views. Concerning Henslow's attempt to explain the origin of adaptive characters, in particular, the development of flowers adapted to insect-mediated pollination by means of the mechanical influence of insects, Timiriazev wrote, "Read Henslow's veritable tome *On the Origin of Flowers,* published last year, and you sense the odor of something mouldy, some idle, long-vanished-from-the-realm-of-science invention, composed of impossible explanations. Read, for example, . . . about the supposed influx of plastic juices into the lower lip of the corolla under the influence of insects butting it with their foreheads, and you cannot help but want to repeat with Darwin—'preposterous!'"[8]

Costantin held the same views as Henslow. Timiriazev published a translation of Costantin book and commented in its foreword that the author, basing himself on data of natural variation in plants, vainly strove "to show the inadequacy of Darwin's explanation of the origin of organic forms and the superiority of Lamarck's viewpoint."[9]

A favorite strategy of proponents of the evolutionary significance of the inheritance of acquired characters was to argue that variations caused by external influences or by the use or disuse of organs require a long time and a great number of generations to become hereditarily fixed. Lamarck and many of his followers right up to recent times used this argument. In particular, one may mention MacBride, Fothergill, and Rudolf Fick. Fick once wrote that "the failure of many experiments to call forth adaptive inheritance over a pair of generations . . . is naturally no proof against the

in Plants (London: John Murray, 1908). One should not confuse George Henslow (1835-1925) with John Stevens Henslow (1786-1861), botanist and geologist who guided Charles Darwin's first steps in natural history research.

[8] K.A. Timiriazev, "Faktory organicheskoi evoliutsii" ["Factors of Organic Evolution"] (1890), in *Soch.* [*Works*], 1938, *5:* 130.

[9] K.A. Timiriazev, preface to his translation of the book by Julien Noël Costantin, *Rastenie i sreda* (*prisposoblenie i evolutsiia*) [*Plant and Environment* (*Adaptation and Evolution*)] (Moscow: 1908), rpt. in K.A. Timiriazev, *Soch.* [*Works*], 1939, *6:* 288. [Neither the French nor the English titles could be verified. Constantin wrote extensively in the area of applied botany and evolution theory. Many of his articles have neo-Lamarckian titles.]

significance of adaptive inheritance in natural evolution. . . over hundreds of thousands of years.''[10] L. Keno thought that if a somatic variation did not become hereditary over the course of a hundred generations, it was not grounds to reject the possibility that it would happen over two-hundred or a thousand generations.

Raymond Hovasse correctly observed that the question of the necessity for such prolonged action by an external factor could not be answered empirically, and he joined Guyénot in the opinion that harping on the time factor was a sophism and evidence of the bankruptcy of Lamarckism.[11]

In addition to the use of indirect data, unconvincing even to the authors who used them, there was no dearth at the end of the nineteenth century and in the first three decades of the twentieth century of attempts to experimentally produce somatogenic hereditary variations.

Listed in preceding chapters are the results of experiments meant to demonstrate the heritability of mechanical injuries and of variations due to unusual temperature, chemical (including immunological) agents, and conditions of lighting and humidity. Rigorously conducted experiments set up to verify reports of such a somatic induction invariably yielded negative results. In a similar fashion, experiments purported to demonstrate the heritability of acquired behavioral traits were refuted. Attempts to produce somatic induction by transplanting ovaries between races of vertebrates or insects possessing different coloration likewise defied success. Experiments with ''vegetative hybridization'' in plants and animals, which originally was considered indisputable proof that soma cells can exert a directed influence on sex cells, met the same fate. Investigation of such reports revealed their lack of any empirical foundation.

Many experiments that addressed the question of the inheritance of acquired characters gave results which were liable to different interpretations by different people. They nevertheless had a great impact. They led to a revision of the strict criteria for proof in experiments of this kind. Based on these new criteria, one may evaluate the results of investigations published earlier only when they include the necessary systematic information. If someone wishes to conduct an analogous experiment in the future, he should carefully observe the same criteria. The criteria are simple but obligatory. The homozygous condition of the experimental source material must be checked by inbreeding, that is, one must demonstrate the absence, over several generations, of variation in those traits by which inheritance is to be judged. If the experiment employs an external influence

[10] Rudolf Fick, ''Wiederholte Bemerkungen über die 'Vererbung erworbener Eigenschaften bei den stammgeschichtlichen Umformungen'''', *Abhandl. Preuss. Akad. Wiss. Phys.-Math. Kl.*, 1939, *no. 1:* 14.

[11] Raymond Hovasse, ''Problèmes de l'évolution,'' in the book by J. Rostand and A. Tétry, *Biologie* (*Encylopédie de la Pléyade*) (Paris: 1965), pp. 1676-1677.

intended to cause variation in the parent individuals, then the influencing agent must be precisely characterized and remain constant in all the verifying trials. One ought to make sure that the agent does not persist in the protoplasm of the egg (in the case of a dye, for instance). Offspring of the modified parents must be transferred to the conditions in which the parents lived before their experimental variations arose. If the same variations appear in the F_1 generation as in the parent generation, then it should be ascertained whether the new traits are retained in successive generations and whether the variation occurs when individuals with the ''acquired trait'' are crossed with ones lacking it. If the trait under consideration is quantifiable, then its appearance in all generations studied should be precisely characterized and the reliability of the difference between experimental and control groups should be shown statistically. An experiment should be reproducible, that is, when repeated under identical conditions, it should yield identical results. With transplantation experiments of gonads or of eggs before cell division or shortly thereafter there are additional considerations. In order to clarify the possible influence of the foster mother on traits of the progeny with a different genotype, it must be ascertained that the progeny are indeed from the transplanted eggs and not from eggs that develop in regenerated ovaries of the mother.

Modern theoreticians of evolution have, for the most part, rejected Lamarckian concepts and accepted a synthesis of the data of genetics and the principle of natural selection. They include R.A. Fisher, S.S. Chetverikov, N.V. Timofeev-Ressovskii, J.B.S. Haldane, I.I. Schmalhausen, N.P. Dubinin, J.S. Huxley, Th. Dobzhansky, G. de Beer, C. Waddington, G.G. Simpson, and E. Mayr. They manage to explain the source of evolutionary adaptation without resorting to an assumption of the inheritance of acquired changes.[12] First of all, it was necessary for them to free themselves from the dichotomy of inherent versus acquired traits. Gavin de Beer gave a graphic example of the weakness of this dichotomy. ''Nothing would seem to be more 'innate' than the pair of eyes that vertebrate animals have had since the Silurian period, 400 million years ago. Yet today a fish embryo made to develop in water containing certain simple salts such as magnesium [lithium—L.B.] chloride develops not a pair of

[12] In the most thorough contemporary summaries of the natural laws and motive forces of evolution the impossibility of transformation of nonhereditary modifications into hereditary changes is considered irrefutably proven and not subject to discussion (see, for example, Ernst Mayr, *Zoologicheskii vid i evoliutsiia* [*Animal Species and Evolution*], trans. and ed. V.G. Gentner and V.N. Orlov (Moscow:1968), pp. 127-128 or is discussed only very briefly in order to show the unsoundness of the latest attempts to prove the inheritance of acquired traits, i.e., Z.I. Berman, K.M. Zavadskii, A.L. Zelikman, A.A. Paramonov, and Iu. I. Polianskii, *Sovremennye problemy evoliutsionnoi teorii* [*Contemporary Problems of Evolutionary Theory*] (Leningrad: 1967), pp. 244, 330-335.

eyes but one single median eye like a cyclops. This shows that the organism's genes are not capable of producing a normal organism unless the environmental factors are also normal. . . . Every character has a genetic basis in the organism's genes without which it would not develop at all and is therefore to that extent 'inherited,' but only partly, because every character is also the result of interaction of the genes with the environment and is therefore also 'acquired'. . . . It should be clear from this demonstration that the expression 'inheritance of acquired characters' is meaningless.''[13] De Beer proposes putting the question differently: can a trait that develops in an organism in response to the interaction between genes and certain environmental factors be realized in its progeny in the absence of the original environmental conditions? From a Darwinian viewpoint, new adaptive traits which depend on changes in genotype (gene mutations and recombinations) arise by chance. If certain of these mutations give their possessor an advantage, then they are preserved in their progeny and serve as the basis for further perfection through natural selection.

Attempts to clarify the genetic mechanism which aids and abets the formation of hereditary adaptations led to the construction of several verifiable hypotheses which were similar in many respects but emphasized different sides of the same phenomenon. James M. Baldwin was one of the first to make such a hypothesis.[14] In his view, the primary result of natural selection was the survival of individuals with a favorable nonhereditary variation. In a population which possesses such a trait, there may arise a mutation with the same phenotypic expression, and the new trait is thereby fixed in heredity. Henry Fairfield Osborn expressed a similar idea at the same time as Baldwin.[15] In vain he tried to describe the mechanism of adaptive evolution without assuming either the inheritance of acquired characters or natural selection. Much later George Gaylord Simpson and C.G. Waddington called this mechanism of the origin of hereditary adaptation the ''Baldwin Effect'' (Baldwin himself proposed the term ''organic selection'').[16]

Fredric Wood Jones[17] and later Leo Shiovich Davitashvili[18] quite un-

[13] De Beer (n. 1), pp. 186-187.

[14] James Mark Baldwin, ''New Factor in Evolution,'' *Amer. Naturalist,* 1896, *30:* 441-451, 536-553.

[15] Henry Fairfield Osborn, ''A Mode of Evolution Requiring Neither Natural Selection nor the Inheritance of Acquired Characters,'' *Trans. N.Y. Acad. Sci.,* 1896, *15:* 141-142.

[16] George Gaylord Simpson, ''The Baldwin Effect,'' *Evolution,* 1953, *7:* 110-117; Conrad Hall Waddington, ''The 'Baldwin' Effect, 'Genetic Assimilation' and 'Homeostasis,''' *Evolution,* 1953, *7:* 386-387.

[17] Frederic Wood Jones, *Trends of Life* (London: 1953).

[18] Leo Shiovich Davitashvili, *Sovremennoe sostoianie evoliutsionnogo ucheniia na Zapade* [*The Contemporary State of Evolutionary Theory in the West*] (Moscow: 1966), p. 120.

justifiably wrote that the Baldwin Effect presupposes the inheritance of acquired traits, when in fact this hypothesis speaks not of the inheritance of modifications caused by external influences but of the replacement of such modifications by mutations having the same phenotypic expression.

Ivan Ivanovich Schmalhausen
(1884-1963)

Richard Goldschmidt showed the possibility of obtaining modifications similar to mutations which had occurred earlier. He obtained such temperature-dependent modification in *Drosophila* and called them ''phenocopies.''[19] Heinrich Friesen discovered that x-rays could also produce phenocopies (''roentgenomorphosis'').[20] Ivan Ivanovich Schmalhausen compared these data with other examples of experimental modifications which paralleled mutational changes in plants and animals, e.g., the montane modifications of many plants compared with their hereditary montane forms (experiments of Bonnier); temperature-induced (experiments of Standfuss and Fischer) and chemically-induced (experiments of Harrison and Garret) melanism compared with hereditary melanism in

[19] Richard Benedict Goldschmidt, ''Gen und Aussencharakter (Untersuchungen an Drosophila),'' *Z. indukt. Abstammungs- und Vererbungslehre,* 1935, *69:* 38.

[20] Heinrich Friesen, ''Rentgenomorfozy Drosophila melanogaster'' [''Roentgenomorphoses in Drosophila melanogaster''], *Biol., Zhurn.* [*Journal of Biology*], 1935, *4:* 687-705.

butterflies; the experimental increase in the surface area of yellow spots in salamanders when raised on a light background (experiments of Kammerer) compared with hereditary natural forms whose yellow spots have fused into a stripe (*Salamandra maculosa f. taeniata*); and others.[21] Schmalhausen thought that besides these instances in which experimental modifications produced phenotypic copies of hereditary traits, the reverse was also possible, that is, mutations could occur and their phenotypic expression could resemble experimentally induced modifications. He called such mutations "genocopies," a term much more expressive than its equivalent, "the Baldwin Effect." He thought that in the course of evolution, replacement of nonhereditary variation by hereditary variation could proceed by natural selection of such genocopies This phenomenon was an essential feature of the widely recognized theory of stabilizing selection. Schmalhausen arrived at this theory by analyzing the abundant factual material available. He started with criticism of neo-Lamarckian and autogenetic conceptions of evolution. In his discussion of neo-Lamarckian views he specially noted the use of "the completely hypothetical and, in fact, incomprehensible mechanism of phylogenetic fixation of physiological reactions in the form of inheritance of acquired traits."[22] In Schmalhausen's words, genetics has refuted the arguments of neo-Lamarckism and has shown that the experimental results obtained were conditioned either by long-term modification or, more often, by unconscious selection acting on genetically mixed material. The school of neo-Lamarckism was likewise not helped by artificial and unreasonable constructs, such as the hypothesis of Ludwig Plate. Without any grounds, Plate postulated a transformation from ordinary to prolonged modifications and from the latter to unstable and finally stable mutations.[23]

From Weidenreich's observations Schmalhausen singled out the useful idea that the survival of an organism depends on whether it is able to react to changed external conditions with appropriate changes. Weidenreich, however, did not carry this idea to its ultimate conclusion; instead of the selection of forms capable of adaptive phenotypic reactions, he spoke of the inheritance of acquired characters, that is, the supposed transformation from modification to mutation.[24] In fact, the ability to react with

[21] Ivan Ivanovich Schmalhausen, *Puti i zakonomernosti evoliutsionnogo protsessa* [*The Course and Natural Laws of the Evolutionary Process*] (Moscow-Leningrad: 1939), p. 46.

[22] Ivan Ivanovich Schmalhausen, *Organizm kak tseloe v individual'nom i istoricheskom razvitii* [*The Organism as a Whole in Individual and Historical Development*] (Moscow-Leningrad: 1938), p. 62.

[23] Ludwig Hermann Plate, "Hypothese einer variabelen Erbkraft bei polyallelen Genen und bei Radikalen. Ein Weg zur Erklärung der Vererbung erworbener Eigenschaften" *Acta Biotheor.*, 1936, Ser. A. *2:* 93-124.

[24] Franz Weidenreich, "Das Evolutionsproblem und der individuelle Gestaltungsanteil am Entwicklungsgeschehen," *Vorträge u. Aufsätze üb Entwicklungsmech.*, 1921, 27.

adequate modification is genotypically conditioned and fixed by selection. Schmalhausen insisted that "no other mechanism can be responsible for the development of adaptive variation than the natural selection of organisms that possess that system most capable of producing those reactions that preserve the organism's life in the given changing conditions."[25]

Analyzing the forms of natural selection, Schmalhausen distinguished two basic types: progressive and stabilizing. Progressive selection preserves deviations from the norm which favor survival in changing conditions; in contrast, individuals which possess traits suited to the former conditions are doomed to extinction. Conversely, stabilizing selection acts in situations when conditions of the environment remain unchanged for a certain period. Since organisms living in this environment are adapted to it, the mutants characterized by more or less significant changes in phenotype are in a less advantageous position than the unchanged, "normal" forms, and therefore, selection eliminates deviations from the norm. Schmalhausen wrote, "In that situation, natural selection will preserve the norm, play the role of a conservative factor, supporting a constancy of traits for the species." Nevertheless, when stabilizing selection acts, new combinations of mutations whose phenotypic manifestations neutralize one another are constantly built up, that is, "a constant reconstruction of genotype without change in phenotype" takes place.[26] This also occurs through a buildup of recessive mutant genes in the heterozygous state. In other words, the capacity in a population for changes in phenotype, which would prove useful under changed conditions, is preserved and not revealed until a certain time. When conditions do change, progressive selection becomes once more indispensible for survival.

When presenting the principles of the theory of stabilizing selection, Schmalhausen mentioned his predecessors, the zoopsychologists Baldwin and Lloyd Morgan and the paleontologist Osborn. Where Schmalhausen, however, explained such phenomena by invoking stabilizing selection, Osborn and Morgan interpreted them from a Lamarckian position in that they accepted the transformation from adaptive modifications ("individual accommodations" in Schmalhausen's terminology) to hereditary changes. Baldwin's ideas did not contradict the Darwinian theory of natural selection, but Baldwin as well as Osborn and Morgan assigned only an auxiliary significance to "organic selection." Schmalhausen, on the other hand, showed that stabilizing selection plays a leading role in evolution "as the principle which through the transitional stage of individual accommodation fixes acquired adaptations and increases the phylogenetic plasticity of the organism."[27]

[25] Schmalhausen (n. 21), p. 89.

[26] *Ibid.*, pp. 48-49.

[27] *Ibid.*, p. 51.

With comprehensive clarity Schmalhausen presented in a series of articles the modern notions of the correlation between genotype and external environment in the evolutionary process. These appeared together in two posthumously published works, the collection *Cybernetic Questions of Biology* and the second edition of *Factors of Evolution.* In an article from the above collection, entitled "Control and Regulation of Evolution," there is an especially important section concerning the significance of the direct influence of external factors in the process of evolution. The hereditary information contained in the fertilized egg or in a cell involved in asexual reproduction experiences transformation in the process of individual development. Despite the complex sequence of morphological and biochemical changes on which ontogenesis is based, the genetic code is reproduced unaltered in all cells, both in those destined to form the future sex elements and in the somatic cells. He saw proof of the preservation of the genetic code in the regular repetition, in each successive generation, of traits inherited from predecessors. While external factors impinge on the mechanism for the transformation of hereditary information in ontogenesis, they do not touch the genetic material. That material is very stable and well protected from chance influences of the environment by the regulatory devices of each individual cell and of the entire organism. Disturbance of the cell's metabolism may exert an indirect influence on its genetic material, but the influence is not specific and its results are the chance, "indefinite" (in the Darwinian sense) hereditary changes called mutations. Mutations in sex cells will be expressed by variations in the progeny that develop from them, and changes in the hereditary material of somatic cells will result in somatic mutations. Mutant progeny will be preserved in the population only in the unlikely case that they pass the test of natural selection. Phenotypic changes that result from external factors disturbing the mechanism for the transformation of hereditary information during individual development are most often unfavorable for survival, since the unchanged, "normal" individuals are adapted to the given environment, while changed individuals are sifted out by selection. Nevertheless, in situations where the phenotypic changes do not hinder survival and where organisms possessing them may propagate, their progeny will again be unchanged, "normal" individuals because their genetic information remained undisturbed. Schmalhausen concluded, "Thus, the inheritance of traits acquired during the life of the individual is practically impossible, since this "acquisition" affects only the transformation of information in the given individual, and dies with that individual. The genetic material is untouched by that transformation and remains unaltered." [28]

[28] Ivan Ivanovich Schmalhausen, "Kontrol' i reguliatsiia v evoliutsii" ["Control and Regulation in Evolution"], *Biull. Mosk. ob-va ispyt. prir.* [*Bulletin of the Moscow Society for Experiments in Nature*], 1958, *63,* no. 5, pp. 93–121, rpt. in I.I. Schmalhausen, *Kiberneticheskie voprosy biologii* [*Cybernetic Questions for Biology*] (Novosibirsk: 1968), p. 65.

Schmalhausen compared phenotypic changes in parents, which resulted from a disturbance in metabolism, that is, a disturbance of the transformation of genetic information, with phenotypic changes in mutant offspring of those parents. Speaking of the non-correspondence of phenotypic changes in such parents and offspring in the same terms used to explain schemes cited earlier (see chapter 11), he showed the unlikelihood of parallel, and especially somatic, induction. He wrote, "There is, of course, no reason to expect that the phenotypic expression of a new mutation will match a phenotype which is the result of a disturbance in the transformation of information, that is, in the process of individual development. Not only are the factors that influence it different, but the material that reacts is different (part of the developing organism, on the one hand, and the genetic material of the chromosomes, on the other). Therefore, a similarity of the phenotype in an altered individual and its progeny would be an extremely unlikely event." [29]

Schmalhausen's carefully thought-out and rigorously argued views confirm, on the level of modern science, the truth of the Darwinian doctrine of evolution, that is, evolution through random variation and natural selection. This conception of the progressive force of evolution makes obsolete all other explanations, in particular, the long championed Lamarckian hypothesis of evolution through direct adaptation.

[29] *Ibid.*, p. 65.

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