Problems of Variation and Heredity in Russian Biology in the Late Nineteenth Century

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The birth of a new science is a complex historical phenomenon having its roots in the remote past. It is the legitimate, although often difficult, task of the historian of science to determine not only the causes behind that event, but why it occurred at a certain time and place.

The founding of genetics in 1900 as a result of the rediscovery of Mendel's laws is one such extraordinary historical episode. The attempts to explain it as a purely "accidental" event not linked with the general development of biology are unacceptable and, indeed, "antiscientific." Nor can the "sudden" emergence of Mendelism be explained by nonscientific —that is, purely political, religious or philosophical—influences. Therefore I cannot agree with the explanation suggested by K. A. Timiryazev[1] that "German chauvinism" and British "clerical reaction" were responsible for the origin of Mendelism.[2] Mendel's discoveries proceeded from and were based upon a long history of experimentation in plant hybridization.[3]

1. See K. A. Timiryazev, *Sochineniia* [Works], vol. VI (Moscow, 1939), pp. 264–265.

2. See A. E. Gaissinovitch, *Zarozhdenie genetiki* [Origins of Genetics] (Moscow: Isdatel'stvo Nauka, 1967), pp. 129–131; idem, "The Rise and Development of Mendelism," [Russian] in A. E. Gaissinovitch, ed., *Gregor Mendel', Sharl' Noden, Ogiusten Sazhre: Izbrannye raboty* [Gregor Mendel, Charles Naudin, Augustin Sageret: Selected Works] (Moscow: Meditsina, 1968), pp. 49–50; and idem, "Clement A. Timiryazev and Mendelism," *Folia Mendeliana, Brno,* 6 (1971), 305–310.

3. See H. F. Roberts, *Plant Hybridization Before Mendel* (Princeton: Princeton University Press, 1929); C. Zirkle, *The Beginnings of Plant Hybridization* (Philadelphia: University of Pennsylvania Press, 1935); A. E. Gaissinovitch, "Gregor Mendel and his Forerunners [Russian]," in Augustin Sageret, Charles Naudin, and Gregor Mendel, *Izbrannye Raboty o Rastitel'nykh Gibridakh* [Selected Papers on Plant Hybrids] (Moscow: Gos. Izd. Biol. i Med. Lit., 1935), pp. 9–155; R. Olby, *The Origins of Mendelism* (London: Constable, 1966); H. Stubbe, *Kurze Geschichte der Genetik bis zur Wieder-*

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The rediscovery and, what is more important, the recognition of the laws established by him could have resulted only from the advances made by biology, beginning in the 1870s, in knowledge of the phenomena of cell-division, fertilization, and embryonic development. Moreover, although the advent and development of Mendelism was not a narrow national event, but rather an international movement which involved many countries, special features and traditions in the study of the porblems of heredity and variation differed markedly from country to country.

Mendelism was recognized in Russia much later than in other European countries, and genetics began to develop as a branch of science only in the Soviet period.[4] This may be accounted for by some historical reasons which have their roots in the previous development of biology in Russia.

In Russia, which followed the example of other European countries, the problems of variation and heredity began to be discussed heatedly in the 1880s, due in great part to the achievements of cytology in studies of fertilization and development, and to the numerous resulting theories of heredity. These theories also contributed to elucidating the regularities of evolution and generated, as is well known, a collision between the old and new interpretations of Darwinism, the new introducing revisions derived from Lamarckian evolution. These discussions exerted a very powerful formative influence upon the attitude of Russian biologists to the new science of genetics which came into existence in the twentieth century. Indeed, the late recognition of Mendelism in Russia cannot be understood unless the "prehistory" of Soviet genetics is considered. Such an account also seems very instructive in light of the recent (1948–1964) anachronistic "relapse" into antigenetic attitudes which took place in the USSR. And, finally, such an account is necessary, as during the above period some serious distortions were introduced into many historical and scientific publications in order to fit into the framework of the tendencies prevailing at that time.[5]

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entdeckung der Vererbungsregeln Gregor Mendels (2nd ed.; Jena: Fischer, 1965); and articles by Gaissinovitch in n. 2.

4. See A. E. Gaissinovitch, "The Beginning of Soviet Genetics. I. The Fight Against Lamarckism (1922–1927) [Russian]," *Genetika, 4,* no. 6 (1968), 158–175.

5. See, for example, I. A. Polyakov, "The Struggle of Russian Biologists against Mendelism [Russian]," *Trudy Instituta Istorii Estestvoznaniia 3* (1949), 3–27; P. A. Novikov, "The Struggle against Weismannism-Mendel-

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It would be only natural to begin an analysis of theories of heredity and variation advanced during the second half of the nineteenth century with a consideration of the influence exerted upon them by the laws of heredity discovered by Mendel (1866). But, as we know, in Mendel's lifetime his discoveries were neglected and few read his work.

It is now known that among the three or four scientists acquainted with Mendel's work during his lifetime was I. F. Shmalhauzen, a Russian botanist (1849–1894). He was the only person who realized and appreciated the great importance of the classical experiments carried out by Mendel, and he described them in his master's thesis "On Plant Hybrids" (1874).[6] Unfortunately, neither he nor any of his Russian contemporaries continued these experiments.

At that time the attention of Russian, and later of foreign biologists, was focused on the experiments conducted by V. I. Shmankevitch (1839–1880), who claimed that he had succeeded in turning the crawfish *Artemia salina* into forms having much resemblance to the allied species of *Artemia Mülhausenii,* and even with the genus of *Branchipus,* by altering the salinity of the water. Shmankevitch, however, was prudent in his conclusions and warned that "it does not mean that the experiment conducted could change one species into another or create new species"; besides, he noted, "the new form developed in such a way cannot be regarded as a new species or variety as its properties are not strong enough to persist in nature." [7] This idea was more precisely expressed in his German publication; he stated there that the variant form of

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ism-Morganism in Russian Zoology [Russian]," ibid., 5 (1953), 93–144; B. E. Raikov, "V. I. Shmankevitch and his Works on the Effect Exerted by the Environment upon the Organism [Russian]," ibid., 5 (1953), 245–272; and the sections in *Istoriia Estestvoznaniia v Rossii* [History of Natural Science in Russia] (Moscow: Akademiia Nauk, 1962) vol. III, by S. L. Sobol (pp. 251–271) and P. A. Novikov (pp. 272–346).

6. For details see Gaissinovitch, "Gregor Mendel and his Forerunners," pp. 127–129; and "The First Account of G. Mendel's Work in Russia (I. F. Schmalhausen, 1874) [Russian]," *Byulleten' Moskovskogo obshchestva ispytatelei prirody (biol.),* 70 (1965), 22–24; and *Zarozhdenie genetiki,* pp. 105–107.

7. V. I. Shmankevitch, "Some Species of Crustacea of Saltlake and Fresh Waters and their Reaction to Environment [Russian]," *Zapiski Novorossiiskago Obshchestva Estestvoispytatelei,* 2 (1875), 1–391, especially 369–370.

Artemia salina obtained by him remained "unchanged as long as its environment is the same." [8] Nevertheless, Shmankevitch held that his experiments could prove that it was possible to form new species by direct and prolonged influence of the environmental conditions. He regarded Darwin's theory of natural selection as a purely logical construct, corroborated only by "indirect evidence." He claimed that the results he obtained allowed one "*not only to imagine* but also to see and feel, i.e. to become fully convinced of, the variability of species, and the improvement of forms resulting from the *natural necessity* of modification impressed on them." Hence, Shmankevitch arrived at the conclusion that "in spite of the great popularity of the widely recognized theory of natural selection, and of other processes leading to alteration and improvement of organisms, many people have good reason to believe that the problem still remains to be solved and that only future generations, by extensively applying physicochemical laws to biological phenomena, will accumulate enough evidence to be able to explain the natural process in the development of organic forms." [9]

The experiments carried out by Shmankevitch were, naturally enough, regarded by the wide circle of biologists in Russia and abroad as a proof of the direct influence of environmental conditions on the process of formation of species. The experiments attracted the attention of Charles Darwin and of Alfred Russel Wallace. In 1881 Darwin wrote to Karl Semper, who had given an account of Shmankevitch's experiments in a book [10] published the previous year:

> Again I was much interested about *Branchipus* and *Artemia*. When I read imperfectly some years ago the original paper I could not avoid thinking that some special explanation would hereafter be found for so curious a case. I speculated whether a species very liable to repeated and great changes of conditions, might not acquire a fluctuating condition ready to be adapted to either conditions.[11]

8. V. I. Shmankevitch, "Über das Verhältniss der Artemia salina Milne Edw. zur Artemia Mühlhausenii und dem Genus Branchipus Scharff.," *Zeitschrift für wissenschaftliche Zoologie*, 25 (1875), 109.

9. Shmankevitch, "Some Species of Crustacea," p. 381.

10. Karl Semper, *Die Natürlichen Existenzbedingungen der Theire*, 2 vols. (Leipzig: Brockhaus, 1880). Darwin read the book in English translation: *Natural Conditions of Existence as They Affect Animal Life* (London: International Science Series, 1881).

11. Charles Darwin, *More Letters*, ed. Francis Darwin and A. C. Seward (London: Murray, 1903), I, 391.

It is quite obvious that Darwin fully understood the idea behind Shmankevitch's experiments and attempted to interpret them not from the Lamarckian standpoint based on the inheritance of acquired characters, but in full conformity with the now accepted conception of the "norm of reaction" of inherited characters.

Wallace's attitude was less clear: he was ready to recognize that "change of form . . . is inherited," but only "while remaining under the same conditions." [12] Of course, this reservation vitiates his assertion that such changes are inherited.

Compared with these and other arguments of Shmankevitch's contemporaries, the statements made by B. E. Raikov in 1953 appear rather ahistorical. He writes that at first Shmankevitch's works "enjoyed full sympathy," which presumably changed completely "only after the extremely reactionary theory formulated by Weismann and the so-called neo-Darwinists" came into existence.[13] However, in the 1870s Weismann himself supported the view that the direct influence of environmental conditions was responsible for changes in the characters of species. Thus he proved experimentally that seasonal dimorphism in coloration and pattern of the wings of butterflies resulted from temperature variations.[14] But he also held at the same time that the very nature of the response of the organism to these influences depended on its inherent potentialities. Weismann supposed that variations in environmental conditions "cause species to change the direction of their development. The complex chemico-physical processes of metabolism gradually change during the chrysalid period to produce both a new pattern and new coloration in a butterfly." [15]

Another experiment was carried out in 1876 under Weismann's direction by Marie de Chauvin, his student. She experimented on transformation of axolotl into amblystoma by artificially reducing their stay in the water medium. Weismann interpreted these transformations as a return to the more

12. Alfred Russel Wallace, *Darwinism* (London: Macmillan, 1889), p. 427.

13. Raikov, "Shmankevitch," p. 264.

14. August Weismann, *Studien zur Descendenzlehre*, 2 vols. (Leipzig: Englemann, 1875–76): vol. 1 was *Uber den Saisondimorphismus der Schmetterlinge.*

15. "Die Entwicklungsrichtung der Art wird eine andere. Die complicirten chemisch-physikalischen Vorgänge im Stoffwechsel der Puppenschlafs verschieden sich allmählich derart, dass daraus als End-Resultante eine neue Zeichnung und Färbung der Schmetterlings hervorgeht." Ibid., I, 43.

ancient form. It is worthy of note that I. I. Metchnikov was an ardent opponent of this explanation, and in 1876 he repeated the experiments on changing axolotl into amblystoma. He believed that changes in the development of the gonads were responsible for the transformation and stated: "The suggested explanation is in sharp contradiction to the view advanced last year by Professor Weismann, who regards the transformation of axolotls as a return to the original salamander-like form, the return resulting from changes in environmental conditions which force axolotls to exchange a branchial respiration for a pulmonary one." [16]

Thus, Darwin and Metchnikov were in their treatment of the role of external factors in the changes of species characters much closer to the future "Weismannism," then were either Weismann at that time or the "Neo-Darwinist" Wallace. This may be the reason why the above statements of Darwin, Wallace, and Metchnikov were not mentioned either by B. E. Raikov or P. A. Novikov, who were seeking everywhere only for the "noxious" influence of the "reactionary Weismannism."

A thorough verification of Shmankevitch's experiments undertaken much later by N. S. Gaevskaya convincingly demonstrated that "various forms of the *Artemia* genus, described as different species, are in reality temporal and local variations of one form." [17] Thus, Darwin was quite right to have interpreted the forms obtained by Shmankevitch as "fluctuating" variations of the same species.

It is a well-known fact that in the 1870s and 1880s considerable progress was made in the study of the intimate processes of karyokinesis (by Strasburger [1875], Flemming [1878–1882], and many others, among them the Russian investigators Russow [1872], Chystyakov [1874–1875], Mayzel [1875–1879], and Peremezhko [1878–1880]), of fertilization (van Beneden [1875–1882], Oscar Hertwig [1875 and later]), and of the role of the nuclear structure in such processes. Proceeding from this a "nuclear" theory of heredity was formulated and numerous hypotheses of heredity suggested. Unlike the hypotheses of the 1860s (Spencer in 1864 and Darwin in 1868), which proved not to be congruent to the real processes

16. I. I. Metchnikov, "Investigations into Axolotl Transformations (1876)" [Russian] in his *Akademicheskoe sobranie sochinenii* [Collected Works] (Moscow: Gos. Izd. Med. Lit., 1955), III, 49.

17. N. S. Gaevskaya, "Variations in Artemia salina [Russian]," *Trudy Osoboi Zoologicheskoi Laboratorii i Sebastopol'skoi Biologicheskoi Stantsii* (Imperatorskoi) *Akademii Nauk*, ser. ii, no. 3.

of gametogenesis and fertilization,[18] new hypotheses (Galton in 1875, Weismann in 1883, and later Naegeli in 1884 and deVries in 1889) took into consideration, to a greater or lesser extent, the dualism of the cellular elements (sexual and somatic) and their structures, and the resulting difference in their fate during the processes of inheritance and development. Especially fruitful in this respect were numerous hypothetical constructs advanced by Weismann, which occasioned heated discussions and conflict of ideas in the 1880s and 1890s. This conflict of ideas drew widespread comment in the Russian scientific press.

The attitude toward Weismann's theories in Russia largely depended on the treatment of problems of evolution. In the 1880s there were in Russia representatives of both "orthodox" Darwinism and extreme Lamarckianism, as well as proponents of various eclectic intermediate positions, among whom were also ranked the determined anti-Darwinists. The most prominent and popular among the orthodox Darwinists was K. A. Timiryazev (1843–1920), known as the Russian "apostle" of Darwin for his popularization of Darwinism beginning in 1864. But with regard to the problem of hereditary transmission, Timiryazev opposed any and all theories of heredity, considering them to be premature and unscientific. As early as 1871, in the "Propositions" appended to his master's thesis on the "Spectral Analysis of Chlorophyl," Timiryazev formulated, following an old tradition, his attitude to every problem in science. He wrote: "The theory of pangenesis is principally unscientific, and unable to yield any results." [19] Timiryazev was set against Darwin's hypothesis of pangenesis, and never ceased attempting to prove that Darwin subsequently abandoned it, a belief which does not correspond to reality.[20] Timiryazev, moreover, disapproved of all the other theories of heredity. He maintained that Darwinism should not become involved in the examination of the regularities of heredity, which should be reserved for a future branch of science, "experimental morphology." Timiryazev vividly formulated this conception of the relations between the phenomena of heredity and the theory of natural selection in his famous speech "Factors of Organic Evolution" (1890). He stated in his speech that "the prevailing tendency of German scientists to create a *general theory* of

18. On this see Gaissinovitch, "Darwin's Views on Variation and Heredity [Russian]," *Iz Istorii Biologii* 2 (1970), 33–59, especially pp. 36–37 and 51–52.

19. Timiryazev, *Sochineniia*, II (Moscow, 1937), 92.

20. See Gaissinovitch, "Darwin's Views," p. 53.

heredity can hardly be regarded as successful or even meeting the real needs of science. A general theory of heredity seems to be no more possible or necessary than a general theory of variation." [21] It is quite natural that proceeding from his attitude he did not consider himself responsible for a detailed study of the problems of heredity. It was much later, after Mendelism came into existence in the twentieth century, that Timiryazev had to become closely involved in the discussion of the problems of heredity, this due to the attempts made in 1909–1916 to use Mendelism against Darwinism.[22] During the period under consideration, Timiryazev concentrated his criticism only against the Russian supporters of an undisguised anti-Darwinism such as N. Ya. Danilevsky (1885) and N. N. Strakhov (1887 et al.).

The vivid articles which I. I. Metchnikov (1845–1916) began to publish in 1875 were a direct contrast to such a treatment of the controversial and unsolved problems of Darwinism. The central place among them is given to his "Essays on the Origin of Species" (1876). Metchnikov is known to have criticized some aspects of Darwin's theory—for example, the role of overpopulation in the struggle for existence, the role of interspecific struggle, and of the continuous and gradual nature of inherited variations.[23]

Metchnikov's treatment of the problems of inherited variations underwent considerable evolution. In 1876 he shared the common conviction in the inheritance of acquired characters. Thus, explaining Lamarck's teaching, he wrote that "the role of *inheritance* in transmitting acquired characters is fully recognized even now." [24] Even Weismann shared the same belief at that time. However, after Weismann postulated in 1883 that acquired characters were not inherited, an explanation which was in full accordance with his teaching on the difference between sexual and somatic cells, Metchnikov seems

21. Timiryazev, *Sochineniia*, V (Moscow, 1938), 138.

22. See Gaissinovitch, "Timiryazev and Mendelism."

23. See Gaissinovitch, "The Great Russian Biologist I. I. Metchnikov [Russian]," in I. I. Metchnikov, *Izbrannye sochinenii* [Selected Works] (Moscow: Utchpedgiz, 1956), pp. 6–30; idem, "Elie Metchnikov et le Darwinisme," *Proceedings of the XVth International Congress of Zoology, London (1959)*, pp. 110–113; and idem, "I. I. Metchnikov, The Great Russian Biologist [Russian]," *Zhurnal Obshchei Biologii, 31* (1970), 490–499.

24. I. I. Metchnikov, "Essays on the Problem of the Origin of Species (1876)" [Russian], in *Akademicheskoe sobranie sochinenii*, IV, 155–327; the quotation is from p. 182.

to have maintained his former convictions, at least as far as bacteria were concerned. Only in later life did he reject, with increasing vehemence, Lamarckian inheritance of acquired characters, retaining only the possibility of its occurrence in the most primitive organisms. In 1901 he wrote: "It is common knowledge that characters acquired during the lifetime are not transmitted to progeny; only in some exceptional cases do the lowest organisms, such as bacteria and their relatives, retain some acquired characters in an infinite number of generations." [25] His statement of 1909 was even more categorical: "While formerly it was taken for granted that any change which occurs in an organism within its lifetime is transmitted to descendants, now quite an opposite conclusion has been arrived at. It has been recognized, mainly under the influence of Weismann's arguments, that acquired characters are not inherited." [26] Nevertheless he cited once again "a typical example of transmission of acquired characters in heredity for anthrax bacteria," [27] but admitting in another passage that "this example does not refer to an organism comprised of several categories of cell, but to one of the most primitive organisms, consisting of one unit or one row of cellular elements." [28]

It was no easier for Metchnikov to accept the new ideas of fertilization, or those of heredity closely associated with it. Proceeding from his observations on the fertilization of jellyfish, in 1886 Metchnikov challenged the argument advanced by Oscar Hertwig and some other investigators that the nucleus of an egg and that of sperm were theoretically the idioplasm conjectured by Naegeli. He could not agree to the assumption of the equal "quantity" of idioplasm in male and female gametes and refused to see idioplasm "only in chromatin." Thus Metchnikov arrived at the deduction that "no matter how important the new conclusions about the processes of fertilization may be, we have not yet advanced far enough to make a mature decision on the problems of the essence of heredity and fertilization." [29]

25. I. I. Metchnikov, *Nevospriimchivost V Infektsionnikh Bolieznyakh* [The Non-Susceptibility of Infectious Diseases] (St. Petersburg: Rikker, 1903), p. 477.

26. I. I. Metchnikov, "Darwinism and Medicine (1910)" [Russian], in *Akademicheskoe sobranie sochinenii,* IV, 404.

27. Ibid., IV. 405.

28. I. I. Metchnikov, "Celebration in Darwin's Honor in Cambridge (1909)" [Russian], in *Akademicheskoe sobranie sochinenii,* IV, 400.

29. I. I. Metchnikov, "Embryologische Studien an Medusen, (1886)," in *Akademicheskoe sobranie sochinenii,* III, 197.

That it was difficult for Metchnikov to apprehend the new ideas in biology of the late nineteenth century, particularly Weismann's ideas concerning the difference between sexual and somatic cells, is the more surprising in that as far back as 1866 he had described the early isolation of sexual cells in insects, which was one of the first proofs of the so called "germ-track" postulated by Weismann.

On the other hand, Metchnikov proved to be very shrewd in his estimation of the role of the saltatory variation in the process of evolution. As is known, Darwin was aware of sudden and abrupt deviations. But he considered them to be important only for the evolution of cultivated plants and domesticated animals. He held, in the first place, that organisms being cultivated by man were subject to a greater influence of environmental changes and were therefore more variable. But more important was the belief that these individual and sharp deviations, according to the conception prevailing at the time of Darwin, could not persist in nature due to the absorbing influence of free intercrossing.[30] Metchnikov absolutely refuted all these arguments. He declared: "Darwin's opposed view in the problem of the sudden origin of species does not hold water, as the evidence he himself has obtained indicates." [31] Metchnikov had in mind in this case the property of "stable inheritence" usually displayed by the suddenly emerging new characters. He wrote: "Hereditary stability of the race characters that have suddenly emerged is a fact constant enough for Darwin to regard it as a general rule." [32] Metchnikov concluded: "The variations that suddenly come into existence have much more chance to stand against the effacing effect of crossing, than minor individual deviations." [33] Thus Metchnikov, far from being disturbed by the "Jenkin's nightmare" that haunted Darwin, was, on the contrary, profoundly convinced of the dominant role of saltatory variations in the processes of natural selection. Metchnikov even reprimanded Darwin for "holding back natural selection for some reason, when considering this problem." [34] "Stability of the suddenly emerged characters greatly contributes to selection, which

30. For details see Gaissinovitch, "Darwin's Views on Variation and Heredity," pp. 43–45.

31. Metchnikov, "Essay on the Problem of the Origin of Species (1876)" [Russian], in *Akademicheskoe sobranie sochinenii,* IV, 247.

32. Ibid.

33. Ibid.

34. Ibid., IV, 248.

does not occur when it is necessary to select among and retain unstable individual variations," stated Metchnikov. After giving examples of useful characters, "that suddenly originate and can be fully transmitted to progeny," Metchnikov came to the general conclusion that "facts resting upon domestic breeds . . . go to confirm the theory of the sudden origin of more or less sharp deviations which can be fixed both due to their own stability and to the influence of selection." [35]

One cannot help being surprised at the extraordinary foresight of Metchnikov, who anticipated our modern conception of the role of mutation in the process of evolution. Therefore it is not surprising that Metchnikov accepted with great interest and understanding the mutation theory that made its appearance at the beginning of the twentieth century. Giving an account of the speeches made at the anniversary celebrations held in Cambridge in 1909 to commemorate the fiftieth anniversary of the publication of the *Origin of Species*, Metchnikov pointed to the disagreements between the "orthodox" Darwinists and the "neo-Darwinists" in the treatment of this problem. Thus, he said, Ray Lankester, the venerable representative of the first, "has quite definitely opposed the theory of sudden mutations, elaborated by de Vries,[36] as well as the results of the investigations into heredity, conducted by Bateson and resting on Mendel's discovery, much spoken about during the few last years." [37] Then Metchnikov concentrated on the problem of the role of "sudden changes" in the process of evolution. He was far from being a supporter of the "orthodox" Darwinists in this question. He wrote: "orthodox Darwinists have supported the thesis advanced by Darwin that species can emerge only as a result of vague individual changes as asserted by Darwin." Then he continued: "according to the orthodox adherents, science has not progressed at all since Darwin's works. But it is an incontrovertible fact that organisms [which are] subject to considerable variations, confirm to a considerable extent changes that occurred suddenly without intermediate stages. Neo-Darwinists resolutely insist on the thesis that it is the sudden changes which provide the greatest

35. Ibid., IV, 249.

36. It is known that even before de Vries, the theory of "discontinuous" variation was substantiated by William Bateson (1894), and in 1899 S. I. Korzhinsky (1861–1900) suggested a theory of "heterogenesis" also based on saltatory hereditary variation. Unfortunately, this theory cannot be discussed in this paper.

37. Metchnikov, "Celebration," IV, 398.

opportunities for natural selection and consequently that 'mutations' have greatly contributed to the origin of species." Then Metchnikov gave examples of the adaptive coloration of insects and flowers, showing that slight differences in coloration were not noticed by insect-eating birds and pollinating insects. Metchnikov concluded: "We can give many other examples illustrating that sudden changes have much more chance to be fixed by natural selection than vague individual changes." [38] As one can see, Metchnikov repeated, almost word for word, his view of the dominant role of sudden changes which he had put forward as early as 1876.

I want to dwell also on the views of another scientist belonging to the "older generation" for whom apprehension of "new trends" was fraught with difficulty. It was P. F. Leshaft (1837–1909), a very original and interesting figure among the Russian evolutionists of the late nineteenth and early twentieth centuries.

Petr Franzevitch Leshaft received his education and developed into a scientist in the 1860s, and for the rest of his life maintained the ideals and traditions of his younger days. He was a fanatical supporter of the then popular mechanical materialism, and was always inclined to reduce all phenomena of nature, including those of organic nature, to mechanical forces, which he regarded as inherent properties of matter. He stated: "The only primary forces whose existence in nature we can assume are attraction, cohesion, resistance, heat, and perhaps electricity." [39] Proceeding from this, he was always distrustful of all the specific organic "forces," properties, and faculties ascribed to living beings or to their structures and functions. According to him, among these were not only vitalistic, teleological, and autogenetic forces and faculties, but also specific properties of individual tissues and organs and of the entire organism. He was inclined to regard inheritance as some "innate power," and treated it with great distrust. Leshaft argued: "It [inheritance] is an unknown faculty or power stimulating a living organism, similar to many protecting and directing metaphysical powers invented by scientists at different times and given various names." [40] Regarding all these explanations of vital phenomena as teleological and un-

38. Ibid., IV, 399.

39. P. F. Leshaft, "Heredity [Russian]," *Russkoye Bogatstvo* (1889), no. 9, pp. 33–80; no. 10, pp. 3–59; no. 11, pp. 98–132; and no. 12, pp. 39–83; quotation from no. 10, p. 15.

40. Ibid.

scientific, Leshaft was convinced that living organisms could not have any adaptive structures or functions which were predetermined by heredity. He stated: "There are no adaptations here which could protect or defend it [the organism] from destruction; everything depends only on the energy of its tissues which alone is responsible for the restoration of the lost balance." [41]

Proceeding from this position, Leshaft could not support Darwin's teaching either. "Natural selection, as Darwin understood it, can only be assumed as an hereditary faculty of a living being for the easier control of obstacles it encounters and thus very useful in the struggle for life. Darwin often attributes to this faculty the importance of an innate power which acts only for organism's good and in its favor. He always emphasizes the hereditary transmission of the faculty or power expediently directing the actions of a creature." [42] But Leshaft did not recognize these powers and therefore rejected Darwin's theory, which rested on such "inherited faculties." Thus, the only theory which could give a really "scientific" (that is, according to Leshaft, "mechanical") and not "metaphysical" explanation, was one which did not tolerate any innate "powers" or "faculties" incorporated in the developing but not yet functioning organism before it confronted its environment. Such a theory, according to Leshaft, was Lamarck's teaching, and it is not surprising that Leshaft was, and continued for the rest of his life to be, its ardent adherent. Leshaft, however, accepted this theory rather idiosyncratically, interpreting it in his own way. He stated: "Jean Lamarck is the founder of the mechanical theory and therefore the founder of real science in its modern meaning." [43] Drawing a comparison between the ideas of Lamarck and those of Darwin, Leshaft suggested that "Jean Lamarck's teaching directly links all the principles and truths obtained by physicochemical science with the study of biological sciences. . . . On the contrary, Ch. Darwin's teaching makes very little use of physicochemical science; the primary importance in Darwin's teaching is attributed to hereditary transmission." [44]

This critical analysis of the two evolutionary theories is very surprising. In any case, not everything that Leshaft says

41. P. F. Leshaft, "Editorial [Russian]," [Proceedings of St. Petersburg Biological Laboratory], *1* (1896), 17.
42. Leshaft, "Heredity," no. 10, p. 15.
43. Ibid., no. 10, p. 42.
44. Ibid., p. 43.

about Lamarck's views is completely correct. Lamarck is known to have been an inconsistent materialist with deistic deviations. But even if his general philosophic views are disregarded, Lamarck's evolutionary conception was not that of "pure" mechanistic ectogenesis. He assumed the existence of an intrinsic factor of "gradation" in living nature which governed a gradual improvement in the organization of living beings; the environment only disturbed and deviated, according to Lamarck, the correct course of gradation. The environment, in his opinion, affected only plants directly; as for animals, they first strove actively to change their behavior ("habits") to make their organs function in an advantageous way, and they therefore changed accordingly. To generate new organs an animal was expected to make "efforts of his internal sense." But the crucial fact was that all the modifications in organs governed by these internal factors could persist and be transmitted to descendants only if they were inherited, a fact established in Lamarck's "Second Law." Ignoring all these aspects of Lamarck's teaching, Leshaft borrowed from him only the principle of use and disuse of parts under the influence of the living conditions of the organism (Lamarck's First Law). This, he claimed, was the universal factor governing the variation of living beings.

Leshaft expounded his general biological concepts in his work "Heredity," published in 1889 as a series of articles in the journal *Russkoye Bogatstvo*. In his later publications he always repeated, sometimes using the same words, the views on the problems of development, variation, heredity, and evolution which he had formulated in this, his principal work on general biology.

In "Heredity" Leshaft subjected to analysis all the theories of development, fertilization, and heredity which had been advanced since ancient times, either refuting them directly or disputing their validity. Proceeding from his primitive mechanistic concepts of the processes of fertilization and development, Leshaft suggested his own original "energetic theory": "The process of fertilization consists in the addition of the energy of the male sexual element to that of the female sexual element, resulting in the activation of the latter which reveals itself as conception." [45]

Very significant in this respect was Leshaft's attitude to the "laws of heredity" established by Haeckel. In 1866 Haeckel

45. Ibid., no. 12, p. 82.

had formulated "laws" of conservative and progressive heredity. He held that "conservative or preserving heredity" was the inheritance of the properties obtained by the organism from its parents and ancestors. "Progressive or increasing heredity," according to Haeckel, was the inheritance of individual features acquired by the organism during its lifetime under the causative influence of its living conditions and development. This was an eclectic attempt to "synthesize" Darwinism and Lamarckism.

In considering these "laws," Leshaft stated: "All these principles cannot be regarded as laws, as they have not been verified well enough and some of them (acquired characters) have even been refuted by the majority of investigators." [46] Thus, the Lamarckian Leshaft did not recognize the inheritance of acquired characters! This followed from a special analysis of facts concerning "transmission of particular properties and capacities." [47] He based his opinion on the work of Wilhelm His and August Weismann, with whom he agreed on this question. Leshaft's analysis of the problem suggests that he was principally unwilling to distinguish between the "innate" faculties and the acquired ones. According to Leshaft, both the former and the latter were formed *anew* in the course of development and owed their qualities to the influence of the developmental conditions, both uterine and extra-uterine ones, and to their upbringing. He concluded, in summary: "Man's capacities acquired in the course of his individual life are not inherited. Supposedly, only the manifestations can be inherited which depend on the temperament and the chemical energy of the tissues of the parents, as well as on the economic conditions and mechanical effects under which the embryo is formed and develops." [48]

Thus, we can see once more that Leshaft excluded any idea of hereditary predetermination of development. He was only prepared to accept hereditary transmission of the "main forms of parents," i.e., typical and specific characteristics. As for individual characteristics and deviations, Leshaft, proceeding from his primitive mechanistic concepts, maintained that the presence of "chemical energy" and excitement (or "temperament"), which guaranteed maximum use and disuse of parts and governed development of individual characteristics of the organism, was quite sufficient.

46. Ibid., no. 11, p. 120.
47. Ibid., no. 10, pp. 43–48; no. 11, pp. 101–106; and no. 12, pp. 69–73.
48. Ibid., no. 7, p. 106.

Much attention has been devoted to the primitive, extremely mechanistic views of Leshaft because, on the one hand, they have been distorted in the literature, and on the other, because they have greatly influenced some of the supporters of Soviet Lamarckism.

V. A. Obukh (1870–1934), for example, founded a scientific society in 1924—"Leninism in Medicine"—with the purpose of popularizing Lamarck's and Leshaft's ideas. And V. L. Komarov (1869–1945), the late President of the Academy of Sciences of the USSR, who while a young man worked in Leshaft's laboratory and was in a way influenced by his views, wrote: "Among our professors the most active Lamarckist was P. F. Leshaft, professor of anatomy . . . all his lectures were permeated with Lamarckism; he was a consistent high-principled materialist and consistently adhered to the principle of causality, substituting whenever possible the principle of natural functions for the principle of expediency." [49] During the period of the ascendency of antigenetic tendencies in the USSR (1948–1964), Leshaft was proclaimed an "anti-Weismannist" and, consequently, a forerunner of the so-called "Mitchurinist" biology.[50] That some authors were led into ahistorical absurdities in apologia of Leshaft's views when attempting to satisfy "Mitchurin's" ideas may be seen clearly from the following quotation: "P. F. Leshaft was a progressive scientist not afraid to attack reactionary views indoctrinated into biology by Weismann and other neo-Darwinists. It *is for this reason* [!] that Leshaft was subject to the perpetual persecution of the reactionary professorate and the tzarist government." [51] As one can see, Leshaft attacked not only neo-Darwinists but even Darwin himself. As for Weismann, Leshaft shared his views that acquired characters were not inherited. The more surprising is that we can come across statements made as late as 1968 that "Leshaft accepted transmission of acquired characters in heredity. Following Lamarck he held that improvement of forms and adjustment to activity are accounted

49. V. L. Komarov, *Lamarck* [Lamarck] (Leningrad: Gosizdat, 1925), p. 142.

50. See, for example, G. G. Shakhverdov, "P. F. Leshaft's Struggle against Weismannism and his Teaching of Heredity, Environment, and Upbringing, in the Light of Mitchurin's Biology [Russian]," *Sovetskaya pedagogika* (1949), no. 4, pp. 44–55; and idem, *P. F. Lesgaft, ocherk zhizni i nauchno-pedagogichoskoi deiatol'nosti* [P. F. Leshaft, A Survey of his Life and Scientific and Pedagogical Activities] (Leningrad: "Znanie," 1950).

51. V. G. Kas'ianenko, *Petr Francevich Lesgaft* (Kiev: Akademii nauk Ukrainskoi SSR, 1950), p. 51. [Italics mine—A.E.G.]

for by gradually increasing use and, finally, by inheritance of all the improved forms and faculties. However, he attached a wider [?!] meaning to inheritance of acquired characters than his contemporaries did." [52]

II

Thus, the "older" generation of Russian biologists was not adequately prepared to accept new ideas intended to explain the phenomena of fertilization, development, and heredity. The "younger" generation received these ideas in a quite different way. Among them were M. A. Menzbier (1855–1935), N. A. Kholodkovsky (1858–1921), and V. M. Shimkevitch (1858–1923), all of whom were ten to twenty years younger than Timiryazev, Metchnikov, and Leshaft, and who were educated and entered science not in the 1860s but in the 1880s, i.e., at a time when new approaches to the problems of biology under discussion began to appear. They responded with great interest and comprehension to the cytological discoveries of the 1870s and 1880s, and to the numerous theories and hypotheses resulting from them. As Russia did not have at that time any special journals in biology, they published their views in the pages of literary-didactic periodicals such as *Russkoye Bogatstvo, Russkaya Mysl, Severny Vestnik,* and *Mir Bozhy,* magazines which popularized new ideas in science.

The first to discuss the problems concerned with heredity was N. A. Kholodkovsky, who published in 1887 and the subsequent few years. He dealt, for the first time in Russian, with Weismann's ideas and theories. In his article "Heredity," published two years before Leshaft's article of the same title, Kholodkovsky analyzed the corpuscular theories of heredity, beginning with Darwin's pangenesis (1868), but revealing a much deeper understanding of the problem.

Analyzing and comparing different hypotheses of hereditary transmission, Kholodkovsky concluded that Weismann's was "the most perfect of all the existing theories of hereditary . . . This new theory of heredity is extremely original and explains many facts. It cannot be regarded as highly speculative, as it is supported by more evidence than any other theory of

52. D. A. Zhdanov, "The Anatomical Investigations and World Outlook of P. F. Leshaft and their Significance for Modern Anatomy [Russian]," in P. F. Leshaft, *Izbrannye trudy po anatomii* [Selected Works on Anatomy] (Moscow: Meditsina, 1968), p. 16.

heredity." [53] Nevertheless, Kholodkovsky found two principal shortcomings in Weismann's and in many other theories of heredity. In the first place, they were purely morphological theories. Thus, Kholodkovsky argued that theories of pangenesis by Darwin and by Brooks (1883) could "be called *morphologic* theories, as they assume the existence of special regular elements (grains) whose functions are responsible for heredity." [54] Weismann's theory, however, rested on the discoveries which established that, "similarly to the main role played by the cell nucleus in the process of fertilization, the carrier of inheritance is, presumably, *nuclein,* i.e., the nuclear substance." [55] Weismann, accordingly, maintained that "egg and semen incorporate specific *germ plasm* of an extremely complex molecular structure concentrated, in all probability, in the nucleus of sexual cell." [56]

Though Kholodkovsky did not challenge these discoveries, he thought that it was impossible to explain the phenomena of heredity proceeding from morphologic elements and structures. "Heredity is a purely physiological, and at the same time, very complicated and delicate process," he stated. In particular, he believed, this theory could not explain the origin of new hereditary properties. Kholodkovsky was convinced that "individual characteristics which were not innate to the parents, but originated in the course of their lives . . . can be 'inherited,'" but the question which interested him was "in what way can the acquired modifications in the various parts of the body affect the molecular structure of sexual cells to be transmitted through them in heredity?" A negative answer given by Weismann did not satisfy him: "The main principle of this theory—that the acquired characteristics cannot be transmitted in heredity—is too daring to endure severe criticism," he stated. This was the second shortcoming of Weismann's theory. Therefore, Kholodovsky concluded: ". . . there is now hardly a theory of heredity deserving its name, i.e., a theory explaining not the forms of the process, but the process itself. A theory of heredity is reserved for the future." [57]

In later articles Kholodkovsky returned repeatedly to the

53. N. A. Kholodkovsky, "Heredity. Essays on Various Problems of General Zoology [Russian]," *Russkoye Bogatstvo* (1887), no. 7, pp. 39–55, and no. 8, pp. 3–19; quotation from no. 8, p. 14.

54. Ibid., no. 8, p. 4.

55. Ibid., no. 7, p. 50.

56. Ibid., no. 8, p. 7.

57. Ibid., p. 18.

problems of heredity. In 1888 he published a long article on Naegeli's ideas. The article was devoted particularly to an analysis of the evolutionary views of Naegeli. Its last pages, however, were given to a comparison of Naegeli's theory of idioplasm and Weismann's theory of germ plasm. It is worthy of note that Kholodkovsky again emphasized his preference for the corpuscular theory, and, in particular, for the nuclear theory of heredity. He wrote: "The idea of idioplasm is, no doubt, a great idea . . . Doubtlessly, there is in the organism some substance containing all the features peculiar to it and able to transmit these features to its progeny." Kholodkovsky further reminded the reader of recently discovered facts concerning the phenomena of reproduction and fertilization and concluded: "Hence the logical conclusion that *nuclein*, the matter of the cell nucleus, is the very substance where predominantly all the vital and heritable characteristics of organisms are concentrated." [58] Nevertheless, he considered that Naegeli's theory of idioplasm had an advantage over Weismann's theory of germ plasm because it did not restrict the concentration of heritable elements to sexual cells and therefore could explain both the phenomenon of inheritance of acquired characteristics and that of regeneration, particularly in plants.

Meanwhile, Weismann's theory attracted the attention of other Russian biologists. Thus, in the same year, 1888, M. A. Menzbier, in his article "The Progress of Biology," devoted much attention to this theory and considered that it had advantages over Naegeli's. He stated: "The difference between Naegeli's teaching and Weismann's theory is similar to the difference between any metaphysical explanation and an explanation resting on evidence." [59] That Weismann refuted the inheritance of acquired characters did not seem to Menzbier as fatal to his theory as it seemed to Kholodkovsky. Menzbier was more concerned with the general problem of the causes which give rise to new hereditary characteristics, asserting that Weismann accepted the fact that "constant and continuous direct influence of environmental conditions can, after all, affect germ plasm." [60]

58. N. A. Kholodkovsky, "The Naegeli/Darwin Theory, Critics of the Theory and Its Further Development" (1888) [Russian], in N. A. Kholodkovsky, *Biologicheskie ocherki* [Biological Essays], E. N. Pavlovskii, ed., (Moscow: Gosizdat, 1923). The quotation is from p. 113.

59. M. A. Menzbier, "The Progress of Biology [Russian]," *Russkaya Mysl'* (1888), no. 5, pp. 184–210; quotation from p. 201.

60. Ibid., p. 199.

In 1891 Menzbier devoted a special article particularly to this question of the "origin of individual characteristic features"; this was the first in a series of articles bearing a common title, "The Present Tasks of Biology." He formulated in this article four types of causes which generate new hereditary characters: "1) They are a consequence of a direct environmental influence; 2) they result from changes occurring in the already existing properties; 3) they are a result of correlation of organs and of the organism's functions in general; and finally 4) they are an effect of differentiation of sexes and of sexual reproduction." [61] Having thus arranged all the types of causes, Menzbier agreed that "from the viewpoint of the theory of heredity suggested by Weismann, the sexual process should be considered the crucial, if not the only, factor governing the development of individual properties of numerous organisms." [62]

Two years later, Menzbier gave a detailed summary of current ideas of heredity. After first illustrating Spencer's and Darwin's theories, Menzbier came to the conclusion that "the idea of explaining the phenomena of heredity by the transmission of material particles from organism to organism is, as far as we can judge, quite correct." Menzbier continued with a speculation on Galton's theory (1875) and stated that Galton had "an idea, rather crudely formulated, of some constant germ substance, which is transmitted from one species to another in the number of subsequent generations." This "idea of the stability of germ plasm" proved to be "quite distinct" in the theory of Weismann, "the author of the last and the most complete theory of heredity." Comparing Weismann's theory with that of Naegeli, he quite obviously preferred the former, stating that Naegeli "had a strange idea of germ plasm or idioplasm, as he called it, and did not relate it to a definite place." After mentioning "the vast microscopic investigations of the late 70s and early 80s," he stated that "they laid the foundation of the first attempts to formulate the theory of heredity, resting upon evidence, whereas formerly it could be based only on conjectures." [63] After describing in addition Boveri's experiments on fertilizing enucleated eggs of sea-

61. M. A. Menzbier, "The Present Tasks of Biology [Russian]," *Russkaya Mysl'* (1891), no. 9, pp. 170–191; no. 10, pp. 182–201; and no. 12, pp. 178–198; quotation from no. 9, p. 179.

62. Ibid., no. 9, p. 188.

63. M. A. Menzbier, "Experience of the Theory of Heredity [Russian]," *Russkaya Mysl'* (1893), no. 10, pp. 208–231; quotation from pp. 214–215.

urchin with sperm of another species (1891), Menzbier arrived at the conclusion: "Thus, there is no doubt that chromatin alone is responsible for the hereditary transmission of characters from parents to children, and, in general, of characters of species of one generation to species of others." [64] Drawing further a comparison between the theories of de Vries, Wiesner, and Weismann, Menzbier spoke out explicitly in favor of the last. "To make his theory more substantial he had to resort to hypothesis. What should be preferred? Opinions, certainly, differ, but personally I concur with Weismann." [65] Menzbier was not at all embarrassed even by Weismann's denial of hereditary transmission of acquired characters. He declared: "It may seem that heredity does not play any role in retaining certain properties of organization, which would impede the adoption of evolutionary teaching. But Weismann does not go as far as that. In his opinion the germ plasm, without absorbing, so to say, the newly acquired properties, changes under the effect of various conditions of environment causing changes of the whole organism." [66] Summing up his analysis of Weismann's theory, Menzbier wrote: "I do not think that nothing will remain of this theory, even in the distant future." [67] The development of genetics in the twentieth century has confirmed Menzbier's predictions, although, interestingly, in the later period Menzbier, like Timiryazev, received Mendelism rather critically.

In 1894 the controversial questions of heredity and evolution were more and more heatedly discussed. This may be accounted for in two ways. In the first place, in 1893 Herbert Spencer and Weismann began a famous polemical exchange which continued into the following year. As is well known, Spencer was one of the founders of neo-Lamarckism; according to him, the key factor of evolution was the direct adaptation of organisms to environment, based on inheritance of acquired characters. Secondly, 1894 saw an authoritative journal on general science—*Nautchnoe Obozrenie*—begin publication in St. Petersburg. In its pages there developed a controversy over the problems of Darwinism and Lamarckism. The principles of Lamarckism were energetically defended by the editor of the new journal, M. M. Philippov (1858–1903), a highly educated and versatile scientist, mathematician, and chemist.

64. Ibid., p. 217.
65. Ibid., p. 219.
66. Ibid., p. 227.
67. Ibid., p. 230.

During the first three years of its publication (1894–1896), the journal showed a lively interest in all the problems of biology, and particularly in those of heredity and evolution. Being an experienced journalist and polemicist, Philippov took every opportunity to criticize Weismann's theory and to defend the positions of Lamarckism. He published articles of both foreign opponents of Weismann (H. Spencer, Y. Delage, W. Haacke, and others), and of Russian ones (M. Ganin, partially, Kholodkovsky, and others). A great number of articles and notes were written by Philippov himself ("Darwinism on Russian Soil," "Letters on Transformism," "Lamarckism," "Problems of General Biology," "New Ideas of Weismann," and many others). In his sharp, polemic articles Philippov criticized Timiryazev, Shimkevitch, Kholodkovsky, and many others. It is rather surprising, then, that Soviet historians of anti-Weismannism did not utter a word about the "anti-Weismannist" activity of Philippov. Only one article published in *Nautchnoe Obozrenie* attracted their close attention, an article which, they proclaimed, was a work "of great importance, as it opposed one of the key views of Weismann." [68] This article, by M. S. Ganin, "The Cell Nucleus as an Organ of Heredity," was a critical analysis of "nuclear" theory.

M. S. Ganin (1839–1894) belonged to the "older generation" of Russian biologists, and his work in the field of embryology was published as early as the 1860s and 1870s.[69] Beginning in 1885 he abandoned his scientific work and teaching, and the article in question, published in *Nautchnoe Obozrenie*, was quite literally his "swan song." It evokes an extremely unfavorable reaction from the modern biologist. Having studied the vast literature on the processes of cell division and fertilization, Ganin arrived at the conclusion that none of the generalizations advanced by the authors of these works had been completely established or generally accepted. Particularly, he could not understand why the nucleus should be given preference over the centrosome. Any division, he noted, began with the centrosome and the "spheres of attraction." Hence, he said, "this organ is the apparatus and mechanism governing cell division." [70] The statement of the equal role in fer-

68. Novikov, "Struggle against Weismannism," p. 114.

69. See L. Ya. Blyakher, *Istoriia embriologii v Rossi s seredny XIXdo seredry XX veka; bespozvonochnye* [History of Embryology in Russia from the Middle of the Nineteenth to the Middle of the Twentieth Century] (Moscow: Izo-vo Akademii nauk, 1959) pp. 81–82.

70. M. S. Ganin, "The Cell Nucleus as an Organ of Heredity (A Critical

tilization of nuclei of paternal and maternal origin did not seem convincing to him. He argued that they could differ greatly in size. Consequently, hereditary masses were not always equivalent.[71] He went on to assert that "in different periods of division the so-called chromosomes are not always of the same length and width." And in general "the substance of protoplasm incorporates a number of organized particles whose organization is much similar to that of chromosomes. Such is, for example, the structure of achromatic filaments." [72] Ganin was also doubtful about reduction division. In the first place, "it is difficult to say with certainty to what extent reduction is a general fact: we lack adequate factual knowledge in this respect . . ." [73] And further he wrote: "If reduction occurs at all, it involves not only chromosomes, but also protoplasm, achromatin, and other components of the cell." [74] And, in general, why should preference be given to the nucleus in considering it the carrier of heredity? The "formations such as chromatophores, chlorophyl, starch grains, and the like are no less independent morphologic formations than the cell nucleus." [75] At the same time it was not self-evident that chromatin was always present in the nucleus and that its form was always the same. Hence: "If notwithstanding such instability of chromatin, the supporters of nucleic theory ascribe to this substance the property to retain and transmit hereditary properties from cell to cell, and from generation to generation, it is difficult to apprehend why protoplasm, centrosome, archoplasm, and many other morphologic components of the cell should not be entitled to the same properties." [76] I could continue indefinitely enumerating the numerous doubts which Ganin entertained concerning all the brilliant discoveries and generalizations made by cytologists and embryologists in the 1870s and 1880s. But no further examples are required to illustrate that we are dealing with a backward and retrograde scientist to whom new scientific facts and ideas are incomprehensible.

Analysis of 'Nuclear' Theory) [Russian]," *Nautchnoe Obozrenie* (1894), no. 28, pp. 872–880; no. 29, pp. 897–905; and no. 30, pp. 929–937; quotation from p. 875.

71. Ibid., p. 874.
72. Ibid., p. 878.
73. Ibid., p. 887.
74. Ibid.
75. Ibid., p. 931.
76. Ibid., p. 936.

The subsequent historical development of biology has absolutely removed all Ganin's doubts and skepticism, and everything that he regarded as "unproved" was long ago incorporated into textbooks on biology, embryology, cytology, and genetics. And this out-of-date complication has quite recently been presented as "an outstanding phenomenon in the history of the struggle of Russian biologists against Weismannism," and "the priority in exposing these scientific and reactionary fabrications" was ascribed to Ganin.[77]

In the same year, 1894, V. M. Shimkevitch began to publish his works on heredity. After delivering a speech devoted to this subject at the celebration of the 75th anniversary of the University of Petersburg, Shimkevitch published it with some alterations as a popular-science article.[78] Unlike Kholodkovsky and Menzbier, he was particularly interested, not in Weismann's theory of "germ plasm" or the hypotheses following from it, but in Weismann's arguments that acquired characters were not inherited. He also wanted to know to what extent these arguments could be supported by experimental evidence. He arrived at the following conclusions:

1. Mechanical changes and damage . . . according to Weismann's elaboration, are not transmitted in heredity.
2. Modifications in the parents' bodies that have occurred as a result of use and disuse of parts are, according to Weismann and contrary to Spencer, Romanes, and others, presumably not inherited either.
3. Weismann postulates that among the modifications brought about by the climate and other influences, only those are presumably inherited which affect the sexual cells, the egg of the female, and the sperm of the male.
4. The parental organisms can exert influence on sexual cells or even embryoes only by poisoning or infecting the embryo with substances found in the blood of the parents . . . Thus sexual cells, or, to be more exact, germ plasm—that is, the substance which is part of these cells and which governs the transmission of hereditary properties—is, according to Weismann, almost completely withdrawn from the influence of the parents' organism.[79]

77. Novikov, "Struggle against Weismannism," p. 112.

78. V. M. Shimkevitch, *Izmeniaemost' i nasledstvennost'*. [Variation and Heredity] (St. Petersburg: Izdanie Peterburgskogo universiteta, 1894) and "The Ancient Puzzle (the Problem of Heredity) [Russian]," *Severnyi Vestnik* (1894), no. 10, pp. 49–64.

79. Shimkevitch, "Ancient Puzzle," pp. 50–51.

As to Weismann's hypothesis, his theories on the structure of germ plasm, and its role in the development, Shimkevitch was rather restrained. The hypothesis of hereditarily unequal divisions was not, he thought, supported by the evidence of experimental embryologists, and thus ". . . the question crucial for Weismann's hypothesis remains unanswered." [80]

As Weismann's hypotheses ultimately rested on the assumption of "molecular units of vital substance," and as his ideas of hereditary changes were based on "molecular alterations at the ripening and fertilization of the egg," Shimkevitch arrived at the conclusion that "the mystery of the laws of heredity is hidden in molecular processes, and we have not yet seen a molecule and have discussed all these processes only hypothetically." [81]

The most detailed account of his attitude toward the phenomena of heredity, and toward Weismann's contribution to our knowledge of them, was given by Shimkevitch in a book published two years later, in 1896. He distinguished among Weismann's views the "zoo-biological" and the "molecular" aspects. As to the first, i.e., the inheritance of acquired characters and the interconnected problems of evolution—specifically, those touched upon during Weismann's polemics with Spencer—Shimkevitch maintained that on the whole Weismann had solved it correctly. The second aspect was to be reserved for the future. However, Shimkevitch agreed that the vast majority of biologists accept the existence of, not proved but nevertheless real, special units between the molecule and the cell.[82]

Thus, in defiance of the assertions of historians, the "anti-Weismannists," our leading biologists of the latter part of the nineteenth century, men such as Kholodkovsky, Menzbier, and Shimkevitch, showed great interest in Weismann's theory and, though they differed in appraisal of its various aspects, they were in general unanimous in admitting its great scientific importance. Thus, in 1897 Kholodkovsky again published a summarizing article on "Heredity" in which he, proceeding from the firmly established evidence concerning the processes of cell division (karyokinesis) and fertilization, spoke with

80. Ibid., p. 63.

81. Shimkevitch, *Izmeniaemost' i nasledstvennost'* [Variation and Heredity], p. 23.

82. V. M. Shimkevitch, *Nasledstvennost' i popytki eë ob'iasneniia* [Heredity and Attempt to Explain It] (St. Petersburg: Izdanie L. F. Panteleeva, 1896), p. 62.

certainty about the nuclear theory of heredity, characterizing it as "a theory enjoying almost universal recognition." [83] Continuing with the problem of the role of sexual cells in the transmission of hereditary characters, the equal participation of male and female nuclei in it, and the difference between the sexual and somatic cells, Kholodkovsky did not mention Weismann's name explicitly, presumably taking it for granted that these facts were generally accepted. On the other hand, he was still greatly interested in the problem of hereditary transmission of acquired characters: "I wonder in what way will the changes that occur in somatic cells affect the offspring, to whom they, obviously, can be transmitted by sexual cells only and not by somatic ones." He emphasized: "It is this very problem that constitutes the crucial event around which theories on heredity rotate." [84] The positive solution did not then seem to Kholodkovsky as necessary and obvious as it had ten years before. In general, he accepted all the key conclusions of Weismann's theory. He noted in the first place, that "we can acknowledge as an established fact that heredity has its specific material base represented by a special substance, which is, presumably, concentrated in chromatin of the cell nucleus"; and, secondly, that "the acquired individual changes involving only somatic cells are not usually inherited." [85]

The support that Kholodkovsky, Shimkevitch and Menzbier gave to Weismann's theory at the end of the nineteenth century has been glossed over by our historians and anti-Weismannists.

Thus, as early as the latter part of the nineteenth century, before Mendelism and genetics came into existence, many Russian biologists perceived the imminent coalescence of the cluster of ideas on the material factors of inheritance which was later given the name of the "chromosome theory of heredity," and had accepted the principle of non-inheritance of acquired characters which had been postulated principally by Weismann and which has been fully proved by modern genetics. As to the opposing of a morphological explanation of heredity to a physiological one, which Timiryazev later suggested as a decisive argument against Mendelism, it is quite obvious to

83. N. A. Kholodkovsky, "Heredity" (1897) [Russian], in Kholodkovsky, *Biologicheskie ocherki* [Biological Essays], pp. 116–142; quotation from p. 119.

84. Ibid., p. 122.

85. Ibid., p. 142.

us that it holds no water. Both these explanations are really very important as they deal with two different aspects, or levels of the phenomena of heredity. The "morphological" explanation provides a basis for the mechanism of *transmission* of hereditary *factors* (or, to use the modern wording, the genetic information) from generation to generation; the "physiological" explanation is essential for finding regularities of *realization* of hereditary *characters* in the individual development of organisms. The "morphological" aspect of the principles of heredity was within easier reach of the experimenter, and due to the nature of the object of knowledge it was destined to be discovered before the "physiological" one. And so it actually happened. The principal difference between these two levels of hereditary mechanisms was for a long time beyond the understanding of scientists and philosophers. It was not realized immediately, even in the first years after the birth of genetics. This was responsible for the accusation of classical genetics, not unfrequently advanced, especially by the philosophers, against the "formal" character of the established regularities. It is only in our own day that the "physiological" approach to the phenomena of heredity has been brought within the range of science.