FACTORS OF EVOLUTION

THE THEORY OF STABILIZING SELECTION

BY
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Foreword, 1986

David B. Wake

On 23 August 1948, the Minister of Higher Education of the USSR, S. Kaftanov, issued a series of orders that had fateful consequences. These orders were the most immediate and far-reaching result of the complete victory achieved by T. D. Lysenko and his followers in meetings of the Lenin All-Union Academy of Agricultural Sciences held earlier that month. During those meetings geneticists as a group were condemned as Weismannist-Mendelist-Morganist idealists who believed in a "mythical hereditary substance—endowed by Weismann with the characteristic of continuing existence, not experiencing development, yet at the same time controlling the development of a perishable body" (Lysenko, quoted in Zirkle 1949). This contrasted with the view of Lysenko and his followers, who emphasized *processes* of heredity and focused on metabolism and the interactions between organism and environment. In fact, the members of the Lysenko group, who fancied themselves Michurinist materialists and Darwinists, were in practice advocates of a simplistic notion of the inheritance of acquired characteristics, who simply ignored structural aspects of heredity such as genes and chromosomes. Under extreme political pressure from the top political echelon, the renowned Academy of Science endorsed the Lysenko approach. The series of orders signed by Kaftanov led to the destruction of Soviet genetics as an active science. Although there had been chilling portents of what was to come (for example, the trials of the outstanding geneticist and plant geographer Vavilov, and his subsequent dismissal and death earlier in the decade), Order 1208 led to mass dismissals of university professors. One of the most prominent victims was Academician I. I. Schmalhausen, professor of Darwinism at Moscow University, and director of the Institute for Evolutionary Morphology (Medvedev 1969).

Schmalhausen, a major figure in Soviet science, had been a leader in efforts to confront the vacuousness of Lysenko's approach. Order 1208 destroyed his career, for not only did it remove his professorship, it also decreed the destruction of his books and his research projects. Lysenko had published a lengthy condemnation of Schmalhausen in *Pravda* (reprinted in Zirkle 1949) shortly before the meeting of the Lenin Academy. He cited sections from Schmalhausen's book *Factors of Evolution* which

led him to assert that Schmalhausen was a pro-Morganist, genetic idealist. Schmalhausen also was selected for special criticism by Academician M. B. Mitin. In a speech delivered at the meeting of the Lenin Academy, Mitin charged that Schmalhausen was a Weismannist who expounded principles of genetics in his evolutionary work (speech reprinted in Zirkle 1949). In the prevailing Lysenkoist political environment this was a devastating accusation. On 6 August, following the attacks of Lysenko, Mitin, and others, an ill and dispirited Schmalhausen addressed the Lenin Academy. He spoke briefly, and rather ineffectually, in his own defense. He did not attempt to speak for modern genetics as a science, but instead argued that he was not a geneticist. His expertise was as a morphologist, embryologist, and phylogeneticist, and he declared that his work bore no relation to formal genetics. At the same time he defended a variety of his views, particularly his concept of stabilizing selection (Zirkle 1949). Nevertheless, in September 1948, Kaftanov wrote in *Izvestia* that Schmalhausen ranked first among the modern Soviet supporters of Mendel-Morgan theories (reprinted in Zirkle 1949). Kaftanov stated that

> Academician Schmalhausen denies the inheritance of acquired characters. He finds that evolution depends upon mutations which originate directly in the germ cells of the organisms and have a quite accidental and indeterminate character, not regulated by the conditions of its life. This idealistic, reactionary theory is fundamentally antagonistic to Darwin's teaching. Nevertheless, Schmalhausen always hid under the banner of Darwinism.

As these events were transpiring, the book you are now holding was being translated into English. It first appeared in the USSR in 1947, having been written during the Second World War, and it was immediately recognized as important and original. Dobzhansky (see his foreword) clearly saw this book as a major component of the advancing synthetic theory of evolution (see especially Adams 1980), supplying an important missing link from the base of comparative anatomy and embryology, and the mechanics of development. These are areas that many have claimed were absent from the grand "Evolutionary Synthesis" (e.g., Coleman 1980; Ghiselin 1980; neither cites Schmalhausen). Ironically, Dobzhansky, who apparently wrote the foreword at about the time the events described above were taking place, complimented Schmalhausen on his command of genetics, and characterized him as "perhaps the most distinguished among the living biologists in USSR."

Ivan Ivanovich Schmalhausen (also written Shmal'gauzen, as it is pronounced in Russian, and Schmalhauzen) was born in Kiev in 1884 and died in Moscow in 1963. He was a student of the famous evolutionary morphologist A. N. Severtsov at Kiev, and was a professor at Voronezh

(starting in 1918), Kiev (from 1921), and Moscow (from 1939). In 1935 he was elected to membership in the Academy of Sciences, and in 1936 he succeeded Severtsov as director of the Institute for Evolutionary Morphology of the Academy of Sciences (now known as the A. N. Severtsov Institute of Evolutionary Morphology and Animal Ecology). He also organized a subdepartment of Darwinism at the University of Moscow. Following his dismissal from his major posts in 1948, Schmalhausen returned to comparative embryological and anatomical research on fishes and amphibians as a senior research worker in the Zoological Institute of the Academy of Sciences, and he became head of the institute's embryological laboratory. Although he slowly regained "respectibility," he did not live to witness Lysenko's dismissal in February 1965 from his post as director of the Academy of Science Institute of Genetics, and the subsequent restoration of modern genetics in the USSR (for additional biographical information on Schmalhausen see Makhotin 1964; Gans 1968; Great Soviet Encyclopaedia 1978; and Jahn et al. 1982).

Schmalhausen was a prolific scientist who in 1948 was at the peak of his productivity and influence. He had devoted the early part of his career to studies of comparative developmental morphology and problems in phylogenesis. He was interested in the origin of terrestrial vertebrates, and published articles dealing with various aspects of this problem from 1913 almost until his death. Increasingly his emphasis became focused on the whole organism. This led to the synthetic phase of his work, starting in the 1930s, and to the publication of a number of books. One of these, *Problems of Darwinism* became a standard Russian textbook and went through at least two editions (the most recent published in 1969). After 1948 Schmalhausen returned to empirical science and accomplished important work on amphibian morphogenesis, especially with respect to ontogenesis of salamanders (he also published on cybernetics). In 1950 he began a series of papers which ultimately resulted in a book published posthumously in 1964 and translated into English with the title *The Origin of Terrestrial Vertebrates* (1968; see review by Wake 1971). This scholarly work prudently avoids issues of genetics and evolution and stresses phylogenesis, and while Darwin, Mendel, Weismann, and Morgan are not cited, neither are Michurin or Lysenko. The distinguished group of researchers associated with Schmalhausen during this phase of his career (Lebedkina, Medvedeva, Regel, Vorobyeva, and others) continues productive work in evolutionary morphology to the present time.

Factors of Evolution deserves a far wider audience than it has received. It is a remarkable achievement for its time, and an excellent example of the scope of Schmalhausen's synthetic abilities. Of the many works associated with the great evolutionary synthesis of the 1930s and 1940s, it may well

be the most comprehensive. Dobzhansky considered it to be "one of the 'basic books' establishing the biological theory of evolution" (quoted in Waddington 1975).

Many issues discussed in *Factors of Evolution* are of current interest in evolutionary biology. The book stresses the organismal level of biological organization. The first section deals with individual variability; Schmalhausen discusses norms of reaction during development, morphogenetic regulation of the developing embryo, and the genetic basis of individual variability. This is a sophisticated approach which emphasizes a genotype-environment interaction, and points out some of its contradictory elements. Schmalhausen's genetic views are modern for the time in which he worked, and he shows the influence of such contemporaries as Berg, Timofeeff-Ressovsky, Dubinin, and others. He cites research of Goldschmidt as well as the work of Fisher, Haldane, and Wright. The focus is never on single loci nor on isolated genes in populations, but on organisms, the interactions that influence their development, and variation among them and its consequences.

Schmalhausen's book is an effective example of a strongly dialectical approach to the study of evolutionary biology. Dialectical methods were largely avoided by other major figures of the period of the evolutionary synthesis. Wright is an exception, but his work was not explicitly dialectical either. In recent years, dialectical approaches have become more explicit and popular. Some examples include Gould 1982a, 1982b; Levins 1968; Lewontin 1974; Vrba and Eldredge 1984; and Levins and Lewontin 1985.

Of current interest is the integration and synthesis Schmalhausen achieves as he moves from the organismal to the genomic level in one direction, and to the populational level in the other. His dialectical approach is evident in his formulation of an explicitly hierarchical biological system, in which forces act in opposition between the different levels. As his preface makes clear, he saw his major task to be the development of a dialectical approach to the study of evolution. One sees this theme repeatedly, as in his view that genetics should be a synthesis of the opposing forces of heredity and change, and in his lengthy evaluation of the conflicting roles of natural selection in producing both change and stability. This hierarchical theme is becoming popular with a number of modern evolutionary biologists (e.g., Gould 1982a; Eldredge and Salthe 1984; Wake, Roth, and Wake 1983; Larson, 1984; and Salthe 1985).

What often has been seen as the principal contribution of the book, and, in some ways, its centerpiece, is the elucidation of the concept of stabilizing selection. The clearly-developed concept of a norm of reaction

established the foundation for his ideas on stabilizing selection. His emphasis was on the autonomous development of organisms, characterized by the increased complexity of the morphogenetic system. He felt that autonomization of development occurred under the influence of stabilizing selection, which involved elimination of perceptible deviations from the norm and a subsequent replacement of external developmental factors by internal ones.

As a morphologist, Schmalhausen was well aware of the structural and developmental stability that characterizes not only species but lineages. To him one of the great problems in evolutionary biology was to understand how selection operated on morphogenetic processes to provide transitions from one stable state to the next during phylogenesis. He saw changes in morphogenetic systems as episodic and temporary, occurring under the influence of what he termed dynamic aspects of natural selection. These changes were followed by the dominating effects of stabilizing selection, by which evolutionary stability was reestablished. He envisioned this stability as resulting from the evolution of a morphogenetic regulating mechanism functioning during development, and he attempted to capture this concept in the term "autoregulation."

During periods in which stabilizing selection is operational (nearly all the time in his view), Schmalhausen envisioned a reserve of hereditary variation being built up in a population. Extended periods of stabilizing selection lead to the continuous strengthening of the regulatory mechanisms producing standard phenotypes. That is, the more extended the period of stabilizing selection, the greater the strength of the autoregulatory mechanisms. But at the same time, the genetic potential for variability (largely unexpressed) continues to accumulate (depending on mutation rate, severity of selection, and other factors). The store of variability determines the evolutionary plasticity of a population. Schmalhausen envisioned harmful mutations and genetic combinations as being immediately and constantly eliminated, so the so-called mobilized reserve is composed of neutral and balanced mutations. He emphasized mutations that have relatively minor effects: modifiers, epistasis, neutral mutations of mixed effect, and neutral mutations of conditional effect. In order for evolution to progress, the variational reserve must be mobilized. The first stage of mobilization is the physical manifestation of the previously unexpressed reserve. This might be caused by homozygosity resulting from inbreeding in small, isolated populations, by destabilization of the regulatory mechanisms of development resulting from environmental variation, or by the direct influence of the external environment on the expression of existing mutations. Schmalhausen always emphasized expression that

would move the norm of reaction in some direction. He saw directional change in evolution as the result of many mutations in a pleiotropic system influencing the expression of the phenotype of the whole organism.

Schmalhausen devoted many pages to morphogenesis. Although concerned with problems of ontogenetic transformations during phylogeny he cites neither von Baer nor Haeckel, and mentions heterochronic changes only in passing. There has been so much progress in these areas in recent years that his work has mainly historical interest now, but throughout there are topics worthy of further investigation. One of these is the idea of autonomization of development, which Schmalhausen sees as being related to the evolution of complex regulating systems under the influence of stabilizing selection.

The final section of the book deals with rate of evolution. Some of the arguments are rather general and speculative. But again this is a novel and original treatment, with some intriguing ideas concerning as yet unsolved problems, such as the nature of apparently "directed" evolutionary processes. The book concludes with a broad overview of the factors of significance in what he terms progressive evolution, and reemphasizes the importance of stabilizing selection.

The sophistication of Russian genetics and evolutionary biology during the 1920s, 1930s, and 1940s was impressive, and one wonders what would have happened had not men like Chetverikov, Vavilov, and Schmalhausen, to name only the most prominent figures, been persecuted and dismissed from their posts. Not only genetics but also evolutionary biology in the USSR failed to develop for almost 25 years following the events of 1948.

I believe that failure to appreciate Schmalhausen's insight also retarded evolutionary thought outside the USSR. Dobzhansky appreciated Schmalhausen's work and its significance, but he was busy making his own synthesis. While Waddington appreciated Schmalhausen's work, the approaches of the two researchers had sufficient similarity in some respects that they were seen as being vaguely competitive, and Waddington cited Schmalhausen minimally (Waddington 1961, 1975). Schmalhausen became aware of Waddington's work only after the book had largely been completed (see Preface), so his citation of Waddington is also scanty. It has been necessary for various researchers to independently rediscover Schmalhausen.

From our modern perspective it is apparent that I. I. Schmalhausen was an original thinker of great depth and insight. Just as evolutionary biologists continue to learn from Darwin's 120-year-old work, so we also have much to gain from careful study of Schmalhausen's 40-year-old synthesis.

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