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Ivan I. Schmalhausen

Die Evolutionsfaktoren
(Eine Theorie der stabilisierenden Auslese)

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INHALT

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VORWORT ZUR DEUTSCHEN AUSGABE

Ivan Ivanovich Schmalhausen (the English rendition of his name) died just as I was beginning my own career (1963), and what I first knew about him was that he worked on salamander anatomy, as did I. He kindly sent me requested reprints of his recent work on vertebral development in salamanders. His short papers in *Zoologiski Zhurnal* [Zoological Journal] dealing with anatomical and developmental features of amphibians and with the origins of amphibians from fishes stimulated me. I did not realize at that time that these papers were a return by Professor Schmalhausen to some of his earliest research in comparative developmental anatomy, and that in the middle part of his career he had produced landmark studies in what might be called evolutionary integrative biology. I soon found his now famous book *Factors of Evolution*, which I came to admire. Much later, I had the privilege of writing a foreword to that book when the University of Chicago Press reprinted it. I think of Schmalhausen as an unsung hero of the early to mid-20th century community of evolutionary biologists. The great wars, revolutions, and political tumult of the first half of that century affected him profoundly, and he surely would have been far better known outside Russia were it not for the factors that led his most comprehensive work to go almost unread in the West at the time it was fresh.

When Schmalhausen's most influential book finally became available in English (1949), the exciting phase of the era of the so-called new evolutionary synthesis was nearly over. His book, which had been written during the early years of the Second World War, was seen as somewhat old-fashioned because it did not cite relevant Western literature, with few exceptions, from most of the previous decade. Furthermore, the translation was apparently imperfect so that what are now seen as obvious connections to and extensions of the new synthesis were not evident to readers.

Schmalhausen had been forced by political realities during the Stalinist-Lysenko era to cease any research that involved genetics. Following a political trial in which he was accused of adopting Weismannian and Morganian genetics, Schmalhausen escaped conviction by arguing that he was an embryologist, not a geneticist, and returned to his earlier research in comparative morphology and phylogenetics. His focus was on the origin of terrestrial vertebrates, but he and other phylogenetically-oriented scientists of his era were handicapped by the absence of a clearly articulated comparative methodology (not to be corrected until developments in the 1960s, e.g. Hennig, 1966). Furthermore, he was preoccupied with a search for ancestors and made direct comparisons between living amphibians and a few selected Paleozoic taxa, more or less ignoring everything in between. There has been tremendous progress in filling the record of transitional

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fossils in recent years, and Schmalhausen's work in this area (notably Schmalhausen, 1968) has not stood the test of time very well. While the quality of the morphological observations from his laboratory was high, the general approach was old-fashioned and is little cited today.

In contrast, the early work of Schmalhausen in comparative developmental biology has had lasting value. My own research has been strongly influenced by research he conducted on salamander limb development and evolution (e.g., Schmalhausen, 1910). He understood better than anyone of his generation the nature of limb morphogenesis. He was especially interested in questions of homology, an enterprise made difficult in the absence of explicit phylogenetic hypotheses. He recognized the importance of variation in development, and showed how one can interpret atavistic traits. In my group we long have referred to one of these traits as „Schmalhausen's m”, for the intrapopulation atavism he labeled m₃ (Schmalhausen, 1917). This particular mesopodial element, present in some Paleozoic amphibians, had through time become incorporated into a larger unit, but its independence recurred with regularity, thereby disclosing its ancestry. We documented the widespread occurrence of this atavism and elaborated its evolutionary and phylogenetic significance, basically followed Schmalhausen's reasoning (Shubin et al., 1995), and later showed its significance as a latent homology in salamander evolution (Shubin and Wake, 2003).

The most significant features of Schmalhausen's *Factors of Evolution* were not well appreciated at the time (Schlichting and Pigliucci [1998] offer a useful perspective on this book). The most profound message of his book is that evolution proceeds through modifications of development. Embryology and development played minor roles, at best, in the emerging evolutionary synthesis of the 1920s to the 1940s, and had Schmalhausen's work been incorporated we would have seen quite a different synthesis, I believe. There were two main points of lasting value in the book. These are, first, a lucid presentation of what we today call norms of reaction – that is, the range of variation produced under different environments during development. He was one of the first to highlight this phenomenon, which he had recognized very early in his career as a developmental morphologist and here extended into a genetical framework as well. He recognized that the wild-type phenotype was in fact a range of phenotypes. This range is constrained and limited, yet the system retains the potential to produce other phenotypes under different environmental conditions (e.g., „Schmalhausen's m”; see above). The second point is what he termed stabilizing selection. His view was that alterations of development changed norms of reaction to first cope with, but eventually, to anticipate environmental stimuli. This view of stabilizing selection is very different than what is meant by the term today. It is close to what is known as the Baldwin Effect or Waddington's genetic assimilation (Crispo, 2007).

When environmental stress „releases” new phenotypes from the reaction norm, selection can operate on the new phenotypes to stabilize a new norm of reaction. His book is filled with empirical examples.

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Today phenotypic plasticity is a large topic in evolutionary biology and we have Schmalhausen to thank for laying important groundwork. Had he not suffered the bad luck of being in the wrong place at the wrong time, he would doubtless be even more admired than he is today. His contributions retain freshness in today's intellectual climate that they did not have for researchers in the 1950s. Schmalhausen's insightful book continues to reward the careful reader.

Dave B. Wake Berkeley, 15. November 2008

REFERENCES

- Crispo, E.: 2007. The Baldwin Effect and genetic assimilation: revisiting two mechanisms of evolutionary change mediated by phenotypic plasticity. *Evolution* 61: 2469–2479.
- Hennig, W.: 1966. *Phylogenetic Systematics*. Translated by D. D. Davis und Zangerl, R. Urbana: University of Illinois Press.
- Schlichting, C. D. & Pigliucci, M.: 1998. *Phenotypic Evolution: A Reaction Norm Perspective*. Sinauer: Sunderland, Massachusetts USA.
- Schmalhausen, I. I.: 1910. Die Entwicklung des Extremitätenskelettes von *Salamandrella kayserlingii*. *Anatomischer Anzeiger* 37: 431–446.
- Schmalhausen, I. I.: 1917. On the extremities of *Ranidens sibericus* Kessl. *Revue de Zoologie (Russe)* 2: 129–135.
- Schmalhausen, I. I.: 1968. *The Origin of Terrestrial Vertebrates*. Translated from the Russian (1964) by L. Kelso; edited by K. S. Thomson. New York: Academic Press.
- Shubin, N. H. & Wake, D. B.: 2003. Morphological variation, development, and evolution of the limb skeleton of salamanders. Chap. 5: 1782–1808, in: *Amphibian Biology*, Vol. 5, Heatwole, H. & Davies, M., eds., Chipping Norton, Australia: Surrey Beatty and Sons.
- Shubin, N., Wake, D. B. & Crawford, A. J.: 1995. Morphological variation in the limbs of *Taricha granulosa* (Caudata: Salamandridae): evolutionary and phylogenetic implications. *Evolution* 49: 874–884.