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Schmalhausen's evolutionary morphology and its value in formulating research strategies

Abstract — Schmalhausen (1884-1963) made important contributions to several biological fields, notably embryology, evolutionary morphology, and evolution. Had his important work on stabilizing selection been available to western biologists at the time of the «evolutionary synthesis» it is likely that he would be seen as one of its important architects. His early work as an experimental embryologist contributed to his development of the concepts of norm of reaction and phenotypic plasticity as important components of evolutionary studies. Brief examples from recent studies of limb and brain evolution in amphibians show how his work retains relevance for formulating research programs.

It is my contention that the great Russian biologist I. I. Schmalhausen (1884-1963), was far ahead of his time in his approach to problems in evolutionary morphology. Contemporaries such as Dobzhansky (1949) knew and appreciated him, but he was mainly ignored by other western biologists, even including Waddington, whose work paralleled that of Schmalhausen in some important respects. Here I review some of Schmalhausen's main contributions and show how his approach has relevance for developing modern research strategies in evolutionary morphology.

Elsewhere (Wake, 1986) I have presented an overview and perspective on one of the two books by Schmalhausen (Factors of Evolution, The Theory of Stabilizing Selection, 1949) that have been translated into English. It is regrettable that more of his work is not readily accessible to western readers, for even the most famous of his books in Russian (Schmalhausen, 1969) remains untranslated. Increased attention has been accorded to Schmalhausen recently, including a biography by his daughter (Schmalhausen, 1988) and interpretations of his scientific approach to evolutionary studies (Allen, 1991; Vorobyeva, 1992). I present only some highlights, derived from Schmalhausen's own work and from the sources cited above (and papers cited in turn by them) that are of special relevance to points I will make in this paper.

Schmalhausen and his Contributions

Ivan Ivanovitch Schmalhausen was a student of the famous comparative anatomist A. N. Severtsov, one of the first true evolutionary morphologists (Adam, 1980). Severtsov was interested in general rules of morphological development and evolutionary transitions in morphology; that is, in regularities, repeated patterns and parallels between ontogeny and phylogeny. These issues were united in a field that he termed «phyloembryogenesis». Schmalhausen's earliest work dealt with comparative studies of limb and fin development in anurans, urodeles, mammals and fishes (Schmalhausen, 1907, 1908a, 1908b, 1910, 1912), and his contributions have been of lasting value.

Schmalhausen was educated as a comparative embryologist and anatomist, and he remained associated with these areas of inquiry throughout the first part of the century. The early part of Schmalhausen's professional career was an intellectually stimulating time for Russian evolutionary biology. He was a contemporary of Chetverikov, whose early studies of geographic genetic variation led to a long-continued tradition and strong point in Russian biology. This was the intellectual environment that also produced Dobzhansky. A prevalent theme was that there was a great store of genetic variation in populations and that populations simply absorbed mutations that came along steadily. Also important was Vavilov, a great botanist whose work is more appreciated now than in the past, and who studied the evolutionary origins of domesticated plants. Vavilov was especially interested in regularities in patterns of plant evolution, and is responsible for the so-called «laws» of homologous series (e.g., Vavilov, 1922). I consider Vavilov to be the father of modern studies of homoplasy.

It was perhaps inevitable that a morphologist interested in evolution would also become interested in the genetic foundation of morphological variation, and Schmalhausen became increasingly recognized, within Russia, as a general evolutionary biologist. He succeeded his old professor as director of an institute in Moscow in 1936, and eventually became Professor of Darwinism in the University of Moscow.

It was Schmalhausen's great misfortune to work during a period of great political uncertainty and tumult. Both Chetverikov and Vavilov suffered political ostracism, and Vavilov disappeared. Schmalhausen himself was denounced during the period of the ascendency of Lysenko and attacks on mendelian genetics in the late 1940's, and he was removed from his professorship (Zirkle, 1949). He was partially rehabilitated later, on condition that he restrict himself to studies of comparative embryology and morphology and avoid genetics. The laboratory he then developed in Moscow made important contributions to our understanding of comparative morphogenesis of vertebrates.

The work that introduced Schmalhausen to the English-speaking community of evolutionary biologists is «Factors of Evolution», translated from the earlier Russian version and published in 1949. This book was written during the Second World War, when Russia was out of touch with developments in the West, and even its publication in Russian was delayed until 1947 (the Russian version is dated 1946, but Dobzhansky [in Schmalhausen, 1949] states that it did not appear until 1947). So, when it reached American and British scientists it appeared to be dated, with few modern references. Despite a laudatory introduction by Dobzhansky, the book really had no immediate impact. It did not even cite Simpson or Mayr, so one can imagine how it was received by these scientists, who considered themselves to be the architects of «The New Synthesis» (Mayr and Provine, 1980); it was largely ignored.

Many of the topics addressed by Schmalhausen are of great interest today: norms of reaction, phenotypic plasticity, morphological stasis, and morphological transitions are just a few of the major items (e.g., Sultan, 1992). I think of his book as the most comprehensive and even the most lasting of the great works of the period of the modern synthesis (that is, of the books published from the late 1930's through the 1950's). Allen (1991) has characterized Schmalhausen's work as that of a true, practicing *dialectical* materialist (as contrasted with a *mechanistic* materialist such as R. A. Fisher and perhaps most western evolutionary biologists). The fusion of mendelian genetics with darwinian natural selection led to a focus on genes and to the reduction of issues once thought to be organismal in nature into component parts. The general assumption of the mechanistic materialists was that the whole is equal to the sum of its parts, with no emergent qualities. Thus, in neodarwinism there is emphasis on environmental change, and on atomistic phenomena that frequently are seen as parts of a mosaic of separate and interacting, but ultimately independent, parts. In contrast, the dialectical materialist position of Schmalhausen (enjoying a current resurgence, although most practitioners are unconscious of the philosophical underpinning) sees the parts so interconnected that they cannot be studied separately (Sewell Wright certainly would have been comfortable with this). Change is seen as a fundamental part of any system; it is not necessarily imposed by outside phenomena but rather is built into the interaction of parts, that is, it is an expected outcome of the organization of the system. The internal forces of change can be understood as interactions of factors that are fundamentally in opposition, but are nonetheless components of the system. Thus, on the one hand, heredity is conservative, while on the other, variation is inevitable and radical in its possibilities. Evolution is the outcome of what might be viewed as the opposing forces of heredity and variation. Furthermore, quantitative changes always lead eventually to qualitative change, so that novelty is an expectation. This can be seen most clearly in the processes associated with allopatric speciation, where quantitative changes eventually result in the qualitative change of reproductive incompatibility. In all of this, historical contigency plays a central role.

Allen (1991) has argued that Schmalhausen was a committed dialectician, not a cosmetic one who was conforming to a prevailing political system. In support of this view, Allen cites Schmalhausen's continuous emphasis on the contradictory forces involved in evolution, and his attempt at a true synthesis between genetics and evolution theory, on the one hand, and embryology (and I would add morphology) on the other. Schmalhausen's dialectical approach is especially clear in his focus on stabilizing and dynamic selection as opposing forces; in fact, one can logically argue that Schmalhausen more than anyone else first presented a full theory of stabilizing selection. In his world view, stabilizing selection simply had to be emphasized.

I assert that the development and utilization of the concept of the norm of reaction has been one of Schamalhausen's most lasting contributions. A norm of reaction is the range of phenotypic expression of a given genotype. Schmalhausen recognized stable (genetically fixed, in essence, and highly predictable) and labile («morphoses» and modifications) traits. Morphoses (or phenocopies, features which are indicative of the potential of the developmental system, and hence also predictable) and modifications, which he thought of as at least potentially adaptive, both usually fall outside the norm of reaction of a genotype, except that some categories of modifications could be within the norm. Stabilizing selection converts labile into stable traits. Selection on morphogenetic processes leads to the internalization of external cues, which stabilizes development and makes outcomes highly predictable. Clearly there is a hierarchical component in this. In a variable environment, norms of reaction change constantly, as stabilizing selection does its work. Viewed in a modern perspective, what is needed is a phylogenetic interpretation of the evolution of norms of reaction, for then we will be able to reach a true synthesis of homoplasy and directional evolution.

Schmalhausen used many examples to show that he was thoroughly familiar with then-current genetics, evolutionary theory, development, comparative anatomy, and paleontology. He attempted a synthesis that was both prescient and extraordinarily perceptive. Regrettably, a truly modern synthesis still eludes us, and it is unclear to me whether this is because we lack sufficient empiricism (the almost daily discoveries in developmental genetics continue to be stunning in their possible implications), or because we cannot see the forest for the trees.

My own research has been influenced by that of Schmalhausen in a number of ways, and I will cite two examples that show how his perspectives shaped my work. The first of these focuses on trait evolution, and indirectly relates to morphoses, modifications, and norms of reaction. The second relates to hierarchical issues in organismal and taxic evolution, and the relation between parts and wholes.

Limb Evolution in Urodeles

Some of Schmalhausen's earliest work dealt with limb development in salamanders. His interest was mainly in morphogenesis, but he was strongly influenced by the classic comparative anatomy practiced in Europe in the early part of this century and therefore framed his study phylogenetically. He was especially interested in the relation of parts to wholes with respect to limbs, in particular, the organization of the mesopodial region, the carpus and tarsus. The mesopodia of salamanders contain a number of elements that arise as mesenchymal condensations which chondrify and, in some taxa, ossify. Development of the region involves segmentation and bifurcation of axes of condensation (for a modern review see Shubin and Alberch, 1986). Two of these axes arise as segmentations (preaxial) and bifurcations (postaxial) from the rudimentary distal long bones (radius and ulna in the forelimb; tibia and fibula in the hindlimb). These axes grow from a proximal origin distally during development. A third arises as an independent distal condensation (preaxial), which spreads postaxially, segmenting and bifurcating to form the digital arch (ultimately giving rise to the distal mesopodials, the metapodials and the digits). The three axes converge in the central postaxial region, where Schmalhausen noted a recurrent variant pattern, the appearance of an additional central element (called by him mediale 3, and hence known to workers in the field as «Schmalhausen's m»). He argued that this element is in the background, so to speak, of the generative dynamics of the limb, and that it can variously be present as a separate element, as an amalgamation with a central tarsal, or as an amalgamation with a distal tarsal. Thus, he was exploring generative rules of development and both the bounds on phenotypic expression and the opportunities presented for the evolution of novelty. This research clearly influenced his later important work on phenotypic plasticity, stabilizing selection, and hierarchical issues in evolutionary biology.

Recently Neil Shubin and I have been exploring patterns of variation in salamander limb development from a phylogenetic perspective. In one recently completed study (coauthored with Andrew Crawford) we examined a large series of specimens of the newt *Taricha granulosa,* collected from a single pond in California that had unexpectedly frozen solid and killed the newts. We examined 452 skeletons, and found that about 95% of the forelimbs and 89% of the hindlimbs has the expected, «standard» organizational pattern of the mesopodials. An enormous number of combinations fusion or separation of the seven carpal and nine tarsal elements can be conceived, but we encountered only 21 carpal and eleven tarsal patterns. We found that five patterns were bilaterally symmetrical, which implies an organismal basis (as opposed to a local developmental irregularity). By far the most common of these patterns, both absolutely and in a symmetrical state, was Schmalhausens's m (in 5.4% of hindlimbs, and as a symmetrical pattern in both hindlimbs in 2.0% of individuals). A phylogenetic analysis disclosed that the presence of m as a discrete element restores an ancestral character, found both in fossil temnospondyls and in basal outgroups among salamander taxa. Thus, m is a phylogenetic atavism, the reappearance of a trait characteristic of ancestral taxa. One other symmetrical state also is an atavism. The three remaining symmetrical states duplicate patterns found elsewhere among urodeles either as rare variants or as fixed, novel, apomorphic states. Interestingly, m plays a role in three of the five most common patterns, either as a free-standing atavism or as a part of an amalgamation that has biomechanical and hence possibly adaptive significance. The apomorphies are morphological novelties that have been related to both developmental and adaptive processes (e.g., Wake, 1991). The critical point is that all of the variants are familiar; evolution tends to run in grooves, with generative processes channeling phenotypic expression. The bounded patterns of variation are the manifestation of a combination of phylogenetic history and developmental constraints. What ultimately becomes fixed in a clade may well represent the working of natural selection on the underlying variation. The variant patterns appear as complete and integrated alternative states, and the selection pressures leading to their fixation could be very weak. Once fixed, the new patterns might be very important, and in hindsight viewed as key innovations which open new possibilities for evolutionary diversification (Larson et al., 1981; Wake and Larson, 1987; Wake, 1991).

Brain Evolution in Urodeles

Brains of salamanders historically have been viewed as very generalized, and many neuroanatomists have referred to them as primitive. Others have observed that they appear to be developmentally relatively undifferentiated. However, there clearly is something wrong with this observation, for in many respects the brains of chondrichthyans and even those of petromyzontids are anatomically more complex than those of salamanders. Furthermore, several parts of the teleost brain are vastly more complex (e. g., the cerebellum) than those of salamanders. So, on phylogenetic grounds it is clear that the salamander brain is secondarily simplified (Roth et al., 1993). In collaboration with G. Roth, K. Nishikawa and others in their laboratories and mine, we have been exploring the reasons for this simplification. It now seems clear that salamanders are, in essence, caught in a phylogenetic and evolutionary trap. On the one hand, they have extraordinarily large genomes, and having large genomes means having large cells (Session and Larson, 1987. On the other hand, they are relatively small vertebrates, and some of them are very small, perhaps the smallest tetrapods; this means that they have to produce a complicated brain in a small space with very large cells, and so something has to give. Neuron packing is nearly as tight as it can be, and there is little glial matter in the smallest species (Roth et al., 1990). The extreme cases of brain simplification are found in salamanders of very small size (several species mature at body sizes less than 20 mm) with the largest genomes and cells. I have argued (Hanken and Wake, 1993) that these small salamanders are biologically very much smaller than their metric size implies, and when comparing taxa that vary greatly in cell size, metric size inappropriately and inadequately expresses biological size. Recently we found that large genomes also mean morphological simplification of brain organization in two other vertebrate clades, frogs and dipnoans (Roth et al., 1994).

Brain organization in amphibians illustrates well the significance of hierarchical factors (relation of molecules, cells, organs and organisms) in evolution. In addition, it shows how misleading it can be to consider isolated parts outside of the context of the whole. It is far more parsimonious to interpret the overall organization of the brain as being directly related to cell size than it is to generate a series of separate explanations for the simplified organization of one part after the other.

Summary

Schmalhausen developed a perspective toward evolutionary biology that is resoundingly modern. He was a through-going darwinian, who understood natural selection theory and applied externalist perspectives throughout his career, but at the same time he was a well trained embryologist who understood the nature of generative rules and interpreted them in an evolutionary framework. Evolutionary developmental biology is only one field that owes Schmalhausen a debt. His contributions were general, in that they dealt with all of organismal evolutionary biology, and I believe that they will be some of the most long-lasting contributions from the period of the late 1930's and early 1940's. During the last decade, and continuing to the present, there has been a rebirth of interest in many of the issues Schmalhausen first raised.

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