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Inferring directions of evolution from patterns of variation: The legacy of Sergei Meyen

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ABSTRACT

In the era of the extended evolutionary synthesis, which no longer considers natural selection as the only leading factor of evolution, it is meaningful to revisit the legacy of biologists who discussed the role of alternative factors. Here we analyze the evolutionary views of Sergei Meyen (1935–1987), a paleobotanist who argued that the theory of evolution should incorporate a "nomothetical" approach which infers the laws of morphogenesis (i.e., form generation) from the observed patterns of variation in living organisms and in the fossil records. Meyen developed a theory of "repeated polymorphic sets" (RPSs), which he applied consistently to describe inter-organism variation in populations, intra-organism variation of metameric organs, variation of abnormalities, heterotopy, changes during embryo development, and inter-species variation within evolutionary lineages. The notion of RPS assumes the active nature of organisms that possess hidden morphogenic and behavioral capacities. Meyen's theory is compatible with Darwin's natural selection; however, Meyen emphasized the importance of other forms of selection (e.g., selection of developmental trajectories, habitats, and behaviors) in choosing specific elements from the RPS. Finally, Meyen developed a new typological concept of time, where time represents variability (i.e., change) of real objects such as living organisms or geological formations.

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1. Introduction

For more than half a century, evolutionary theory was constrained by doctrines of the modern synthesis (MS) as formulated by Simpson, Fisher, Dobzhansky, Haldane, Wright, and Mayr. The hallmark of the MS is the assumption of a fundamental asymmetry between genotype and phenotype: mutations in the genome lead to new phenotypes and eventually cause evolutionary changes, whereas the changes in the phenotype have no consequences in evolution. As a result, MS became a gene-centric theory, where the phenotypes were largely ignored. The mathematical models of selection based on MS directly assigned fitness values to various genotypes bypassing phenotypes (Fisher, 1930). But now, due to the progress in molecular and developmental biology, we finally have a better understanding of how phenotypes do emerge, and how are they transferred across generations. The emerging new theory goes under the name of extended evolutionary synthesis (EES), which widens the range of factors beyond the monopoly of natural selection in explaining the directions and rates of adaptive evolution (Pigliucci and Müller, 2010). Because this theory often grounds the emergence of new phenotypes in the mechanisms of embryo development, it is also known as "Evo-Devo" (Brakefield, 2011; Laubichler, 2009).

In periods of rapid scientific expansion, as we experience now with the theory of evolution, it makes sense to revisit the legacy of biologists who discussed alternative theories, and whose work was often ignored. In this paper we analyze the evolutionary views of Sergei Meyen (1935–1987), a Russian paleobotanist who attempted to explain the emergence of various morphologies and patterns of phenotypic variability in macroevolution. Meyen acknowledged the importance of natural selection in adjusting organs and tissues to specific functions, but he argued that natural selection does not explain major patterns in macroevolution. Thus, he proposed to augment the theory of evolution with a "nomothetic" approach, which infers the laws of polymorphism from the observed patterns of variation in the existing organisms as well as in fossil records (discussed in Section 2). Etymologically, "nomothetic" means "lawgiver" (Greek: νομοθέτης); according to Wilhelm Windelband (1904), the nomothetic approach captures general features of the objects of study, whereas the (opposite) idiographic approach is focused on specific details. According to Meyen, the laws of polymorphism do not contradict traditional approaches to evolution (which

Abbreviations: EES, extended evolutionary synthasis; MS, modern synthesis (of evolutionary theory); RPS, repeated polymorfic set.

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include natural selection, environmentally-induced modifications, and developmental correlations), but complement them (Section 3). This approach presented evolution in the context of its changing biotic and abiotic environment. Finally, Meyen turned to the methodological aspect of evolution by asking the question "what is the meaning of time in biological and geological reconstructions?" Taking the notion of time as *durée* from Henri Bergson, he developed a new typological concept of time, where time represents variability (i.e., change) of real objects such as living organisms or geological formations (Section 4).

2. Searching for the laws of polymorphism – a nomothetic approach

The Russian school of evolutionary theory and genetics never adopted the notion of a purely random variation, which is the cornerstone of the MS. Instead, variability was viewed in the context of internal capabilities of organisms manifested in their embryo development and physiology. Lev Berg viewed evolution as a "nomogenesis", a process controlled by laws of morphogenesis (Berg, 1969). Alexey Severtsov developed a theory of evolutionary progress which augmented internal capacities of organisms (Severtsov, 1939). Ivan Schmalhausen introduced the notion of "stabilizing selection" which means selection for phenotypic plasticity and robustness (Schmalhausen, 1949). In contrast to the negative "purifying" selection that eliminates deleterious alleles, stabilizing selection plays a positive and constructive role in evolution.

Meyen's worldview was formed under the strong influence of Alexander Lyubishchev who was an entomologist with a keen interest in the theory of systematics and a follower of Berg. Lyubishchev argued that the cladistic approach was not acceptable because it reduced the taxonomy to the order of bifurcations in evolving lineages and did not account for the integrity of each taxonomic unit (Lyubishchev, 1982). Instead, he promoted a nomothetic approach to systematics, which was targeted at capturing generic laws of polymorphism and allowed the existence of polyphyletic and combinatorial classifications. The idea of combinatorial system originated from the formulation of the "homologous series in variation" by Nikolai Vavilov, who found that phenotypically similar species of grasses often belong to several phylogenetically separated genera, which indicates the existence of morphogenic potential in producing these phenotypes (Vavilov, 1922).

Meyen enthusiastically accepted the main idea of the nomothetic approach, which uncovered the order in a vast variability of organic forms (Meyen, 1973). He applied it to his major subject of study: ancient conifers which dominated during the Mesozoic era (Meyen, 1984a). Publications of Meyen expanded our understanding of the diversity of early conifers of Permian and Triassic periods. Meyen noticed that different phylogenetic lineages of ancient conifers often developed nearly identical morphological structures despite drastic differences in other organs. Moreover, these were not just single cases of similarity but repeated (i.e., parallel) patterns of organ modification found in various species of each taxon. For example, the evolution of tracheids (elongated cells used for transporting water and mineral salts) in ancient clubmosses, rhyniophytes, and other plant lineages progressed independently through the stages of circular thickening of cell wall, spiral thickening, ladder-like thickening, and continuous thickening with pores (Meyen, 1971). Each organ has its own internal pattern of evolutionary change. For example, the variability of possible leaf shapes follows the pattern in Fig. 1 (Meyen, 1973). The evolution of leaves appears to follow its own "internal logic", where possible modifications include three basic types: (a) splitting the end into two branches, (b) producing feather-like nodes, or (c) palm-like

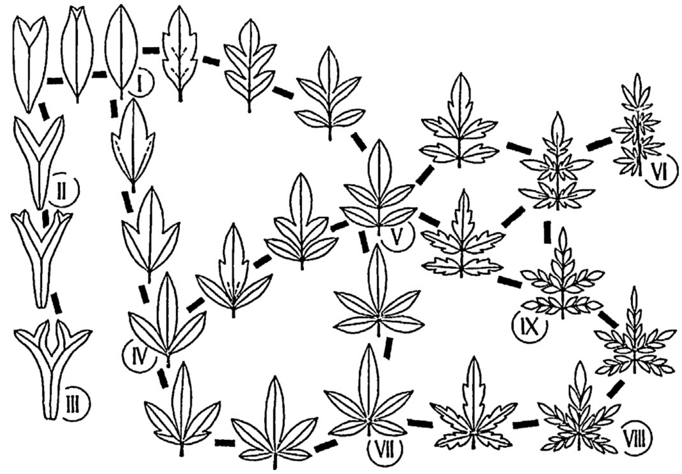

Fig. 1. Scheme of segmentation of leaves (up to the 2nd order of branching), from Meyen (1973).

nodes. These modifications can be applied repeatedly to the products of previous modifications. Different types of modifications can be generated sequentially as shown in Fig. 1; but some combinations are prohibited. For example, a two-branch split at the tip of the leaf is never combined with feather-like or palm-like branching. These transitions are dynamic and their occurrence may depend on the genetic background of a species, stage of development, or environment.

To describe such patterns of morphological variation Meyen uses the term "polymorphic set" which is a set of morphological modalities (e.g., leaf types) connected by certain relations (e.g., order or transformation). If a polymorphic set is repeated in different groups (e.g., taxons, metameric parts of the body, life cycles, or ecological communities) then it is called "repeated polymorphic set" (RPS) (Meyen, 1973). The concept of RPS is similar to Vavilov's term "homologous series in hereditary variations" (see above). However, Vavilov's term is both ambiguous and narrowly defined because (1) it refers to homology which is not always clear, (2) some RPSs may not form series, (3) RPSs are not always heritable (e.g., phenocopies), and (4) the term "variation" is ambiguous because it refers both to the process and result of variation (Meyen, 1973). RPSs are present in the inter-specific polymorphism, intra-specific polymorphism (e.g., phenotypic plasticity, mutation- and stress-related changes, as well as accidental malformations), and even intra-organismal variations in organism components (e.g., segments, leaves, and hairs) or in organ shapes at different stages of organism development. In particular, they include "the law of related deviations" (also known as Krenke's rule) established by Krenke (Krenke, 1933–1935). According to Krenke, abnormal morphologies, either heritable or non-heritable, may closely resemble normal morphologies in related taxonomic groups. Thus, abnormal morphologies indicate the existence of specific morphogenic capacities in organisms, which may appear utilized in the evolution of organisms in another lineage. Moreover, they allow biologists to predict potential directions of evolutionary change towards morphologies that are yet unknown (Meyen, 1973, 1974).

In reference to Krenke's rule, Meyen emphasized the existence of specific structural laws embedded in living organisms, which can be inferred from the systems study of organic forms. Such studies should integrate the knowledge on the extant and fossil organisms in their developmental and evolutionary dynamics, and may include formal descriptions that specify body components, their relationships and symmetry. Then, the change of morphology can be described as a change of composition (i.e., emergence or