



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



Alexei A. Sharov<sup>a,\*</sup>, Abir U. Igamberdiev<sup>b</sup>

<sup>a</sup> National Institute on Aging, Genetics Laboratory, Baltimore, MD 21224, USA

<sup>b</sup> Memorial University of Newfoundland, Department of Biology, St. John's, NL A1B 3X9, Canada

## ARTICLE INFO

### Article history:

Received 9 May 2014

Accepted 16 June 2014

Available online 27 July 2014

### Keywords:

Nomothetic approach

Morphogenesis

Embryo development

Epigenetic regulation

Biological time

Phylogenetic reconstructions

## 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 “nomothetic” 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.

Published by Elsevier Ireland Ltd.

## 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 synthesis; MS, modern synthesis (of evolutionary theory); RPS, repeated polymorphic set.

\* Corresponding author. Tel.: +1 4105588556; fax: +1 410 558 8331.

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

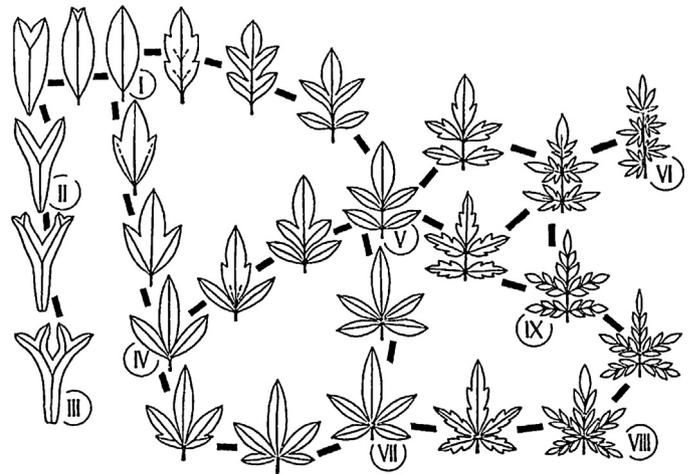


Fig. 1. Scheme of segmentation of leaves (up to the 2nd order of branching), from Meyen (1973).

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

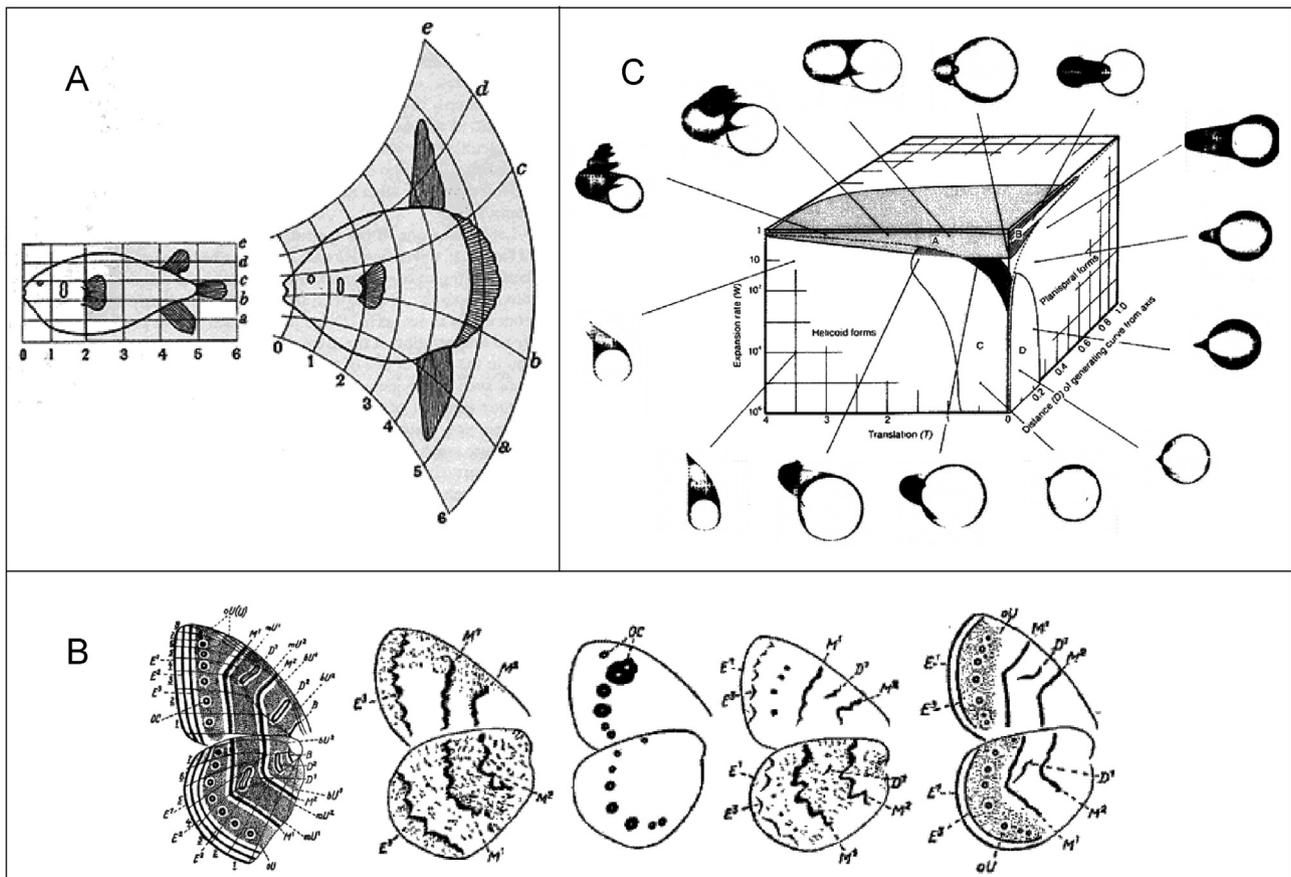
disappearance of system components) and/or rearrangement of relations between these components. A special case of such transformation is a recursive application of polymorphism rules to sub-components following the principle of self-similarity, which is common in fractals. For example, the diagram of leaf shapes (Fig. 1) can be easily expanded by adding 3rd-order and 4th-order branching. However, in contrast to mathematical fractals, self-similarity in nature is never complete and only major qualitative (e.g., topological) characteristics are preserved but secondary quantitative characteristics may vary. Thus, the analysis of forms should focus first on the qualitative invariance, and only then add quantitative characteristics if they are conserved in RPSs. These ideas were inspired by the works of Urmantsev who assumed that every form is plural in nature and belongs to some set of polymorphic modifications (Urmantsev, 1971, 1986). Urmantsev proposed the notion of “bioisomery”, where different morphologies are mapped into one another with conserved (or partially-conserved) relations between components.

Meyen was not alone in exploring the laws of polymorphism in living organisms. D’Arcy Thompson (1917) in his pioneering book “On Growth and Form” showed that shapes of different kinds of fish can be converted one into another by non-uniform stretching or shrinking (Fig. 2A). In other words, shapes of fish differ mostly by distance relation between parts. Boris Shvanvich identified major patterns of bands and eyespots on butterfly wings and their variation (Shvanvich, 1949) (Fig. 2B). David Raup proposed a formal model of snail shape, which is known as “snail cube” (Raup, 1966) (Fig. 2C). Such geometric representation of variability is now called “morphospace” (Brakefield, 2011).

### 3. Combining laws of polymorphism with other factors of evolution

Although Meyen emphasized the nomogenetic (i.e., structural) approach to the study of biological forms following traditions of Berg and Lyubishchev, he admitted that this structural method does not capture other important aspects of embryo development and evolution, such as functionality of organs, adaptability, and the mechanisms of change. Traditional approaches in biology, which account for the history (i.e., origin), function, and adaptation (i.e., ecology and environment) of organisms, provide invaluable information about the manifold of organic forms. Indeed, no form can be fully understood outside of its history, function and environment. But these approaches should be complemented by the structural studies of RPSs (Meyen, 1973). Meyen argued that sets of existing phenotypes of organisms cannot be reduced to their history, function, and adaptation because the same structure often appears in unrelated lineages, the same function can be performed by different organs, and there are many ways to survive in any specific environment. In other words, there is no one-to-one correspondence between these factors. He wrote:

“This means that morphological laws in plants cannot be learned by way merely of historical, functional and adaptational (ecological) analysis of plant forms and structures. We have to study the laws as such (just as in the art sciences Roman pottery may well be studied outside of its utility). In other words, morphological laws cannot be reduced to history, function and adaptation, just as biology itself cannot be reduced to physical and chemical factors.” (Meyen, 1973) (p. 253).



**Fig. 2.** Examples of the laws of polymorphism: (A) transformation of fish shape, from D’Arcy Thompson (1917); (B) prototype of the Nymphalidae wing pattern (left image) and its realization in various species of Erebia (right 4 images), modified from Shvanvich (1949); (C) a model of snail shell shapes (“snail cube”), modified from Raup (1966).

Thus, the traditional evolutionary theory (i.e., MS) is inadequate in its attempt to explain biological forms by a single mechanism—natural selection. But in contrast to Berg, Meyen did not deny the importance of natural selection. He published his vision for a synthesis between nomogenesis and selectogenesis in the paper “Relation of nomogenetic and tycho-genetic aspects of evolution” (Meyen, 1974). The term “tycho-genetic” (from Greek τύχη: chance) was proposed earlier by Lyubishchev to denote the random components of evolution (Lyubishchev, 1965). These two aspects of evolution complement each other in the same way as do categories of necessity and chance. Nomogenetic components appear in a canalization of evolutionary transformations, whereas selection of specific elements from a RPS and its modality may depend on chance (e.g., mutation or environmental change). Thus, morphological transformations in a sequence of generations include both directional and random heritable changes, and natural selection is needed to adjust organs for specific functions. Meyen wrote that the main difference between selectionism (i.e., MS) and nomogenesis is in the way they explain the origin of phenotypic similarity acquired independently in the evolution of several lineages (Meyen, 1974). Selectionism assumes that such similarity arises via natural selection when organs are optimized to perform the same function in the same environment, whereas nomogenesis explains it (first) by universal internal laws of polymorphism, and (second) by the selection of specific forms within RPSs (i.e., tycho-genesis). Meyen used the term “selection” in a broad sense as a set of constraints or guides that contribute to the choice of a specific form within RPS (Meyen, 1975). It includes Darwin’s natural selection (i.e., differential reproduction), selection of behavior, selection of a habitat, and selection of a developmental direction in embryonic organs and tissues. All kinds of selection have important evolutionary consequences (Sharov, 2014). Even non-heritable selections may change the rates and directions of evolution because they modify organism functions and reshape the fitness landscape. For example, new behaviors can facilitate the change of functions via the Baldwin effect (Baldwin, 1896).

Among different kinds of selection mechanisms, Meyen was primarily interested in epigenetic processes. He rejected the “biochemical monism”, a widely held belief that genes and their products determine the morphology of developing organisms. Instead, he wrote that genes function as selecting factors which release or repress the pre-existing morphogenic capacities of the embryo (Meyen, 1973). The existence of such capacities follows from the ability of mammalian embryos to develop major body components before genes become active. In attempt to explain the nature of the morphogenic capacities of the embryo, Gurwitsch developed a theory of morphogenetic field, where changes in the embryo are explained by cell interactions and collective movement patterns (Fig. 3A) (Gurwitsch, 1944). This view was further

developed by Waddington, who proposed a metaphor of epigenetic landscape. The fate of a cell (or tissue, organ) emerges as a trajectory of a ball that rolls along the valleys separated by ridges in a ragged landscape, whereas genes modify the local topology of valleys and ridges, and in such indirect way, change the phenotypic outcome of the developing organism (Fig. 3B) (Waddington, 1957). In other words, genes select stable trajectories of cell development (called “chreods”) at specific unstable bifurcation points designed for epigenetic control. Epigenetic capacities of cells and organs provide opportunities for populations to adapt to changing environments and develop novel functions (Sharov, 2014).

The theory of Waddington is compatible with Meyen’s nomothetic theory. Indeed, the existence of multiple alternative chreods supports the theory of RPSs because the independent emergence of similar morphologies and polymorphic sets can be explained by the similarity of epigenetic landscapes in related species, genera, and families (Meyen, 1974, 1975). Meyen assumed that RPSs have epigenetic nature and are associated mostly with changes in gene functions rather than in the sequence of structural genes. He wrote that the temptation is strong to treat the phenomenon of RPS as polyphyly. However, if multiple instances of polymorphic sets were generated by the shared plesiomorphic epigenetic generative mechanism, then polyphyly vanishes (because polyphyly assumes the full independence of origin) (Meyen, 1984a).

Because cells in different parts of the body change following the same epigenetic landscape, the action of genes is not necessarily restricted to specific organs. Thus, novel morphologies may emerge due to changes in epigenetic control, which results in activating genes in unusual parts of the body. Such changes may be induced by environmental factors or mutations (called “homeotic”), and in the latter case, the changes may become heritable. The outcome of homeotic mutation is not determined by the DNA change because many alternative mutations in various regulatory regions can generate the same effect within the common epigenetic landscape. Expression of regulatory genes in unusual locations may result in relocation or duplication of a specific organ (e.g., eye or leg), a phenomenon called heterotopy. Meyen assumed that heterotopy is a widespread phenomenon and can be used for evolutionary reconstructions. He hypothesized that the shift of fructifications of gymnosperms from leafless fertile shoots to vegetative fronds (e.g., from Lagenostomales to Trigonocarpaceles in the Cycadopsida lineage) can be explained by heterotopy (Meyen, 1984a). He reasoned that the initial heterotopy can be followed by progressive morphological changes caused by ontogenetic correlations and re-adjustment of body parts. This kind of change (Meyen called it “postheterotopic”) is seen in the Ginkgoopsida lineage, where the shift of the synangia and seeds onto the leaves was followed by the modification of microsporophylls and phyllospersms (Meyen, 1984a). According to

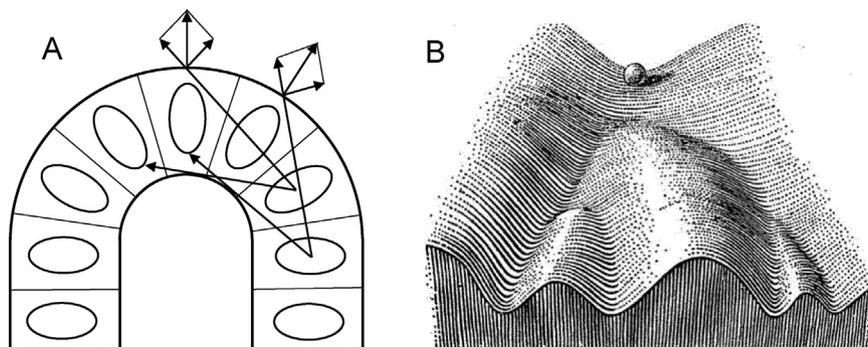


Fig. 3. (A) Field vectors at the rip of archenteron invagination of the sea-urchin, from Gurwitsch (1944); (B) epigenetic landscape, from Waddington (1957).

Meyen, postheterotopic modifications may also include simplification of repositioned organs.

Meyen was interested in the phylogenetic relationships between all major lineages of plants. In particular, he proposed that angiosperms may have originated from bennettites (Meyen, 1988, 1992). He viewed the development of a carpel and reception of the pollen by the stigmatic surface as most important features of angiosperms, even more important than the presence of a flower (Meyen, 1984a). Male fructifications of the oldest angiosperms were not bisexual (as most normal flowers). Meyen hypothesized that bisexual flowers may have originated via gamoheterotopy, which is a transfer of characters from one sex to another. According to this hypothesis, the microsporophyll structure of bennettites (i.e., male sporangia) was transferred to the seed-bearing organ, which resulted in the emergence of a flower-like bisexual reproduction organ. This hypothesis is supported by the deep similarity between bennettites and angiosperms in the morphology of wood, pollen and stomata. It is still considered as a very plausible explanation – 30 years after it has been formulated (Specht and Bartlett, 2009).

Although Meyen emphasized the importance of spatial relations between parts in the epigenetic regulation of morphogenetic processes, he warned against potential oversimplification in inferring causal relationships. In some cases, the whole is more important than parts in determining the morphological outcomes. The effect of individual parts can be overridden by the compensatory regulations at the organism level. For example, perfect organs may develop from varying of heterogeneous parts or predecessor structures. This effect, which was named “non-statistical regulation” by Belousov (1971), indicates the independence of the whole from its constituent parts (Meyen, 1973).

Although evolution follows the laws of polymorphism, the selection of specific forms often depends on the environment and on the presence of ecological niches. Thus, Meyen became interested in the analysis of plant evolution at the planetary scale. When he plotted the geographic distribution of higher taxa from the Silurian to the Quaternary period, it became obvious that all major evolutionary events occurred in the tropics, followed by the spread of newly formed taxa into the north and south non-equatorial regions (Meyen, 1986, 1992). This pattern fits to the hypothesis of “equatorial pump”, which was introduced by Darlington (1959) and can be traced back to Dobzhansky (1950). The formation of new taxa in equatorial regions may have been facilitated by a weak abiotic component of natural selection (Meyen, 1992). If favorable climate preserved rare morphological variants, these variants might appear to be intermediate forms in the evolution towards new perspective types of organization, and became the founders of large lineages. The selective advantage of these forms may increase later in evolution when modified structural and functional components become adjusted and self-regulated. High biodiversity in the tropics may also have contributed to the process of macroevolution via creating novel ecological niches and facilitating speciation via physical separation of subpopulations. Thus, Meyen proposed that the tropics represented the major arena for macroevolutionary events in the evolution of vascular plants. During periods of warming, the newly formed taxa spread to the extraequatorial latitudes, where they continued to evolve and produced more specialized sublineages or became extinct. The opposite process of spreading of boreal species into tropics never occurred. However, some ancient forms could survive for long periods in the extraequatorial regions; this phenomenon is known as “extraequatorial persistence”. The average ages of taxa increase with latitude, with the tropics harboring both old and young taxa and higher latitudes progressively lacking in younger taxa (Meyen, 1992). The process of biospreading is stimulated by natural fluctuations

of climate, such as recurrent glaciations followed by warming periods. Jablonski et al. (2013) generalized that most lineages tend to originate in the tropics and then expand to higher latitudes while retaining their tropical presence. For example, there is extensive evidence on the tropical origin of lineages of bivalve molluscs (Jablonski et al., 2006). Dowle et al. (2013) showed that species density is higher in the tropics than in temperate regions resulting in a latitudinal biodiversity gradient. These and other (Brown et al., 2004; Krug et al., 2009) recent developments of the biospreading concept reinforce the importance of the original ideas of Meyen.

#### 4. The “typological” concept of time

Meyen was a rare scientist who routinely searched beyond the common logical and experimental toolbox. His studies of fossil plants led him to a rather unusual question “what is time?” The paradox of paleobotany is that answers to questions “when?” and “what?” appear to coincide. If some evolutionary event happened in the Triassic period, then the exact physical/astronomic time does not matter. “Triassic period” is the answer to both questions, “when?” and “what?” Thus, Meyen reasoned, time represents variability (i.e., change) of real objects such as living organisms or geological formations, rather than being an abstract background to which other changes are projected (Meyen, 1983). He wrote: “From the observer’s point of view, time is the variability of each object (individual) in the environment . . . We have to consider general features in variability of some set of individuals because we are interested in receiving information concerning not individuals but classes of individuals (taxons)” (Meyen, 1982; pp. 365–366). Most evolutionary theories presume that living systems develop and evolve in the external physical space–time, which is independent and absolute in the Newton’s sense. In contrast, Meyen assumes an alternative view (which goes back to Aristotle) that time is relational and all biological systems have their own individual times, and that embryo development and evolutionary changes include interaction and continuous rescaling of individual times.

In studying the biological time, Meyen follows the same nomothetic principles that he used for the analysis of organism morphology (Meyen, 1983). As leaves of a plant represent different elements of a RPS, the stages of sequential system change fit into some dynamic RPS. Examples of dynamic RPSs include stages of cell cycle (mitosis and meiosis), stages of development of the whole embryo of specific parts (e.g., leaves, sporangia, flowers, fruits). These dynamic RPSs are shared by classes of similar individuals undergoing similar changes. Because detection of similarity includes the reconstruction of a common type, Meyen called his theory “typological concept of time”. Classical morphology is static and generally assumes that change destroys the form. In contrast, Meyen views dynamic RPS as a higher-level “dynamic” form (e.g., represented by cell cycle or life cycle). Thus, time is a creative factor rather than just destructive (Meyen, 1982). Qualitative changes are more important in the dynamics of living systems than mere quantitative changes because they are associated with certain novelties (e.g., new parts, relations, or functions). Similarly, the geological change is partitioned into qualitatively different periods and eras. The study of time is focused on identification of rules (or logic) of system change which can be used for predicting possible and actual sequences of transformations.

Because living systems can be recursively divided into smaller parts, and each part has its own dynamics and own time, the biological time is hierarchically structured (Meyen, 1983). Subsystems at different hierarchical levels have certain spatial and temporal bounds and specific rules of change. For example, these

rules are different for cells, organisms, and populations. On one hand, the hierarchical structure of objects and their corresponding times permits certain freedom in the change of parts at various time scales, from short-term embryo development to the long-term evolution. But on the other hand, the hierarchy implies the importance of synchronicity between parts if they interact and participate in a common function. In this way, the specific time of the whole system cannot be reduced to individual times of interacting parts, but instead represents a higher level coordinating module. Rescaling of internal times of interacting objects leads to heterochrony and may result in spatial shifts of morphology (i.e., heterotopy) (Igamberdiev, 2014).

Physicists consider time as an independent variable, but in the typological concept it appears to depend on external factors. Because interactions between systems may affect their individual times, changes cannot be described simplistically as trajectories in a phase space. Instead, system change appears a superposition of possible trajectories. One of the most common kinds of interactions is synchronization which is the adjustment of time to the change in some other system, living or non-living. Diurnal and seasonal cycles of plants and animals are adjusted to corresponding rhythms of the environment, whereas seasonal cycles of parasites fit the seasonal cycles of their hosts. Coordination between individual times of system components results in the emergence of the integrated time of the whole system, which can be quantitatively represented as one or several principal components within the coordinate system of individual processes (Sharov, 1995). For example, growth or aging is not uniform among parts of the body; nevertheless, the principal component would integrate multiple aspects of growth/aging. Projection of individual times on principal components allows prediction of all the processes with acceptable accuracy. Principal components, which generalize individual events and decrease the number of dimensions, are important for understanding the difference between the process and the time. Each process can be plotted against the time by using projection to the subspace formed by principal components.

The typological concept of time can be used for historical reconstructions (e.g., in geology or paleontology) (Meyen, 1984b). Patterns of variation or change in one kind of systems (or their parts) can be extrapolated to another similar or related kind of systems (or parts). In some cases, structural series of variations (e.g., annual rings on fossil trees) can be used to reconstruct the dynamics of tree growth which is not observable directly (Meyen, 1984b). Fossil records provide information on various stages of organism development and growth, and can be used to reconstruct the whole process of the life cycle. Meyen suggested to call this “processual” reconstruction as “Bergson’s principle” to honour Henry Bergson, who argued that duration (*durée*) cannot be reduced to a succession of distinct instantaneous states (Bergson, 1917). The peculiar feature of fossil records is that they do not provide any hint on the order of “frames” in a “movie” of organism development. Moreover, each stage of development is often represented by unconnected parts such as leaves, fruits, and stem fragments. Thus, the puzzle of processual reconstruction appears to be multi-dimensional and requires the integration of both spatial and temporal relations.

Phylogenetic reconstructions are even more challenging than reconstructions of the life cycle. Relatedness between fossil organisms is not observable and has to be reconstructed from incomplete morphological data (Meyen, 1984b). Criteria of homology between organs are not always clear, especially considering the existence of heterotopy and postheterotopic modifications. Thus, Meyen emphasized the importance of developing multiple scenarios of evolutionary descent; he called it “the principle of Chamberlin”, named after famous

American geologist, who applied it to geological reconstructions (Chamberlin, 1965). This approach helps to avoid subjective preferences of certain hypotheses and provides an opportunity to optimize model selection.

## 5. Conclusion

The major accomplishment of Meyen is his theory of RPSs, which he applied consistently to various biological phenomena such as inter-organism variation within populations, intra-organism variation in metamerous organs (e.g., segments, leaves), recursive variation at different scales of the same organ (e.g., sequential segmentation of leaves), variation of abnormalities (both natural and induced), heterotopy, stage of embryo development or organ development, inter-species variation within evolutionary lineages, and sequential changes of morphology along evolutionary trajectories as reconstructed from fossil and contemporary organisms. Meyen’s “nomothetical” approach infers the laws of phenotypic change from the observed patterns of variation in organisms. Because organism’s morphology recurrently emerges during the ontogeny, the embryonic and postnatal development provides the evidence about hidden morphogenic capacities of organisms and for reusing existing organs for new functions. The notion of RPS follows directly from the active nature of organisms and their components, which exhibit a wide range of morphogenic and behavioral capacities. That is exactly what is missing in the MS of evolutionary theory, which follows the obsolete metaphors of “passive copying” and “sieve” of natural selection. Meyen’s theory is fully compatible with Darwin’s natural selection; however natural selection is not viewed as a sole positive factor of evolution. Instead, Meyen proposed that various kinds of selection (including natural selection) are needed to select specific modalities within RPS and match them to living functions. Finally, Meyen applied his RPS concept to the dynamic variation of systems which he viewed as time of individual real systems, such as life cycles of organisms, evolving lineages, and transforming geological formations. The nomothetic concept of evolution developed by Meyen represents a basis for the synthesis of different factors operating during the evolutionary process, in which the processes spanning from the molecular to the biospheric level globally interact and produce certain directionality of the evolutionary dynamics.

## Acknowledgements

This contribution of A.A.S. was supported entirely by the Intramural Research Program of the National Institute on Aging (NIA/NIH). However, the content of this paper is not endorsed or suggested by the funding organization.

## References

- Baldwin, M.J., 1896. A new factor in evolution. *Am. Nat.* 30, 441–451.
- Belousov, L.V., 1971. Problem of the Embryonic Form-building. *Izdatel'stvo Moskovskogo Universiteta, Moscow* (in Russian).
- Berg, L.S., 1969. *Nomogenesis: Or, Evolution Determined by Law*. MIT Press, Cambridge, MA (orig. 1922).
- Bergson, H., 1917. *L'Évolution Créatrice*. Alcan, Paris.
- Brakefield, P.M., 2011. Evo-devo and accounting for Darwin's endless forms. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 366, 2069–2075.
- Brown, J., Gillooly, J., Allen, A., Savage, V., West, G., 2004. Toward a metabolic theory of ecology. *Ecology* 85, 1771–1789.
- Chamberlin, T.C., 1965. The method of multiple working hypotheses: with this method the dangers of parental affection for a favorite theory can be circumvented. *Science* 148, 754–759.
- D'Arcy Thompson, W., 1917. *On Growth and Form*. Cambridge University Press, London.
- Darlington, P.J., 1959. Area, climate, and evolution. *Evolution* 13, 488–510.
- Dobzhansky, T., 1950. Evolution in the tropics. *Am. Sci.* 38, 209–221.
- Dowle, E.J., Morgan-Richards, M., Treweek, S.A., 2013. Molecular evolution and the latitudinal biodiversity gradient. *Heredity* 110, 501–510.

- Fisher, R.A., 1930. *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford.
- Gurwitsch, A.G., 1944. *The Theory of Biological Field*. Nauka, Moscow (in Russian).
- Igamberdiev, A.U., 2014. Time rescaling and pattern formation in biological evolution. *Biosystems* . <http://dx.doi.org/10.1016/j.biosystems.2014.03.002>.
- Jablonski, D., Belanger, C.L., Berke, S.K., Huang, S., Krug, A.Z., Roy, K., Tomasovych, A., Valentine, J.W., 2013. Out of the tropics, but how? Fossils, bridge species, and thermal ranges in the dynamics of the marine latitudinal diversity gradient. *Proc. Natl. Acad. Sci. U. S. A.* 110, 10487–10494.
- Jablonski, D., Roy, K., Valentine, J.W., 2006. Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science* 314, 102–106.
- Krenke, N.P., 1933–1935, *Somatische Indikatoren und Faktoren der Formbildung, Phänogenetische Variabilität, Abh. Abt. für Phytomorphogenese, Inst. für Biol. I. Bd., Moskau, Moskau*, pp. 11–415 (in Russian, German summary).
- Krug, A.Z., Jablonski, D., Valentine, J.W., Roy, K., 2009. Generation of Earth's first-order biodiversity pattern. *Astrobiology* 9, 113–124.
- Laubichler, M.D., 2009. Form and function in *Evo Devo*: historical and conceptual reflections. In: Laubichler, M.D., Maienschein, J. (Eds.), *Form and Function in Developmental Evolution*. Cambridge University Press, New York, pp. 10–46.
- Lyubishchev, A.A., 1965. Systematics and evolution, intraspecific variation of terrestrial vertebrates and microevolution. *Proceedings of Allunion Conference, Sverdlovsk*, pp. 45–57 (in Russian).
- Lyubishchev, A.A., 1982. *Problems of Form, Systematics and Evolution of Organisms*. Nauka, Moscow (in Russian).
- Meyen, S.V., 1971. From the History of Plant Dinasties. Nauka, Moscow (in Russian).
- Meyen, S.V., 1973. Plant morphology in its nomothetical aspects. *Bot. Rev.* 39, 205–260.
- Meyen, S.V., 1974. Relation of nomogenetic and tycho-genetic aspects of evolution. *Z. Obshch. Biol.* 35, 353–364 (in Russian).
- Meyen, S.V., 1975. Problem of directionality of evolution. *Itogi Nauki i Tekhniki* 7, 66–117 (in Russian).
- Meyen, S.V., 1982. Methodology of the Study of Temporal Relations in Geology, Development of Time Concept in Geology. *Naukova Dumka, Kiev*, pp. 361–381 (in Russian).
- Meyen, S.V., 1983. The notion of time and typology of objects (in geology and biology, as an example), In: *Dialectics in Sciences about Nature and Man*. Nauka, Moscow, pp. 311–317 (in Russian).
- Meyen, S.V., 1984a. Basic features of gymnosperm systematics and phylogeny as evidenced by the fossil record. *Bot. Rev.* 50, 1–111.
- Meyen, S.V., 1984b. The principles of historic reconstructions in biology, In: *Systemness and Evolution*. Nauka, Moscow, pp. 7–32 (in Russian).
- Meyen, S.V., 1986. Florogenesis and evolution of plants. *Priroda* 47–57 (in Russian).
- Meyen, S.V., 1988. Origin of the angiosperm gynoecium by gamoheterotropy. *Bot. J. Linnaean Soc.* 97, 171–178.
- Meyen, S.V., 1992. Geography of macroevolution in higher plants. *Soviet Sci. Rev. G (Geol.)* 1, 39–70 (orig. 1987).
- Pigliucci, M., Müller, G.B., 2010. Elements of an extended evolutionary synthesis. In: Pigliucci, M., Müller, G.B. (Eds.), *Evolution – The Extended Synthesis*. MIT Press, Cambridge, MA.
- Raup, D.M., 1966. Geometric analysis of shell coiling: general problems. *J. Paleontol.* 40, 1178–1190.
- Schmalhausen, I.I., 1949. *Factors of Evolution: The Theory of Stabilizing Selection*. Blakiston, Philadelphia, PA.
- Severtsov, A.N., 1939. *Morphological Regularities of Evolution*. Izdatel'stvo Akademii Nauk, Moscow, Leningrad (in Russian).
- Sharov, A.A., 1995. Analysis of Meyen's typological concept of time. In: Levich, A.P. (Ed.), *On the Way to Understanding the Time Phenomenon: The Constructions of Time in Natural Science. Part 1. Interdisciplinary Time Studies*. World Scientific, Singapore, pp. 57–67.
- Sharov, A.A., 2014. *Evolutionary constraints or opportunities?* *Biosystems*. <http://dx.doi.org/10.1016/j.biosystems.2014.04.005>.
- Shvanvich, B.N., 1949. *Course of General Entomology*. Sovetskaja Nauka, Moscow, Leningrad (in Russian).
- Specht, C.D., Bartlett, M.E., 2009. Flower evolution: the origin and subsequent diversification of the angiosperm flower. *Ann. Rev. Ecol. Evol. Syst.* 40, 217–243.
- Urmantsev, Y.A., 1971. Specifics of spatial and temporal relation in living nature. In: Mostepanenko, A.M. (Ed.), *Space. Time. Motion*. Nauka, Moscow, pp. 215–241 (in Russian).
- Urmantsev, Y.A., 1986. Symmetry of system and system of symmetry. *Comput. Math. Appl.* B 12, 379–405.
- Vavilov, N.I., 1922. The law of homologous series in variation. *J. Genet.* 12, 47–89.
- Waddington, C.H., 1957. *The Strategy of the Genes: A Discussion of Some Aspects of Theoretical Biology*. Allen & Unwin, London.
- Windelband, W., 1904. *Geschichte und Naturwissenschaft*. Heitz, Straßburg.