Alternative evolutionary theories: A historical survey

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Abstract   Our overview has the objective of making our study relevant to bioeconomists. The need for the 'alternatives' to the Synthetic Theory of Evolution in social-economic studies was substantiated, for example, by Colombatto (*Journal of Bioeconomics*, 5, 1–25, 2003), who maintains that the natural-selection theory is 'ill suited' to describing evolutionary processes in economics. He proposed an alternative 'non-Darwinian' approach by equating the 'non-Darwinian' approach with a definite version of neo-Lamarckism. Yet, as we will show, there is a palette of alternative approaches within and beyond the neo-Lamarckism. We hope to give bioeconomists more choice in their theoretical modeling and constructing of analogies between biology and economics. It will also be shown that in the light of suggested definitions the concept of 'universal Darwinism' recently discussed in bioeconomics makes little sense as a generalizing category. In addition, in the concluding part of the paper we demonstrate that the majority of alternative approaches are far from being pigeonholed as archaic and once and for all wiped off the theoretical landscape. On the contrary, in recent years one can observe some revival of interest in the theoretical 'heresies'.

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Darwinism

JEL Classification   10

1 Introduction

The first objections against Darwin's (1859) theory of evolution were announced
immediately after its appearance. The opponents questioned, for instance, the adaptive
character of evolution, the gradualness of evolutionary changes, and the random
character of variation. Discussions around these and related topics gave rise to the
establishment of explanatory models explicitly opposed to the Darwinian selection-
ism. Darwin's death in 1882 only intensified the manifold debates between supporters
and critics of his evolutionary theory. Between 1859 and the turn of the century the
evolutionary biologists concentrated mainly on the evidence for evolution as a fact
and on the phylogenetic reconstructions. In the following years, up to the establish-
ment of the Synthetic Theory of Evolution (STE) in the 1930s and 1940s, the exact
causal relations of evolutionary events (the issues of direct and indirect inheritance,
the role of mutation, geographic isolation, selection or questions concerning evolu-
tionary progress) became the focal point of discussions between various scientific
schools. By the early 20th century, the identification of Darwinism with selection the-
ory 'was becoming widespread in both Britain and America' (Bowler 2004). At the
same time, due to the incomplete and sometimes even contradictory data of palaeontol-
ogy, anatomy/morphology, biogeography, systematics, and genetics, the reconstruc-
tion of evolutionary history still had to be provisional and even speculative (Gould
1977; Nyhart 1995).

Accordingly, at the beginning of the twentieth century the Darwinian theory of
natural selection became just one of the more or less plausible hypotheses of how evo-
lution proceeds (Junker and Hoßfeld 2001). Every country and every single branch
of biology developed in this context its own specific characteristics, which, either
hindering or promoting, affected the national scientific developments in evolutionary
biology (Mayr 1984; Bowler 1992).

The controversies over Darwinism nourished the self-confidence of Alternative
Theories of Evolution (ATE). Therefore the first third of the twentieth century became
the heyday of ATE, which were flourishing at the same time in various countries
and around that time achieved clarity and conceptual maturity. The Swedish historic-
an of biology Erik Nordenskiöld (1872–1933) noted in this connection: 'The history
of biology might really close with the establishing of the dissolution of Darwinism'
(Nordenskiöld 1928, p. 574).

A comprehensible definition of the 'alternative theories' requires a clear distinction
between alternatives and the explanatory models they are opposed to. Such a differ-
entiation became actually possible only with the occurrence of the STE, which pro-
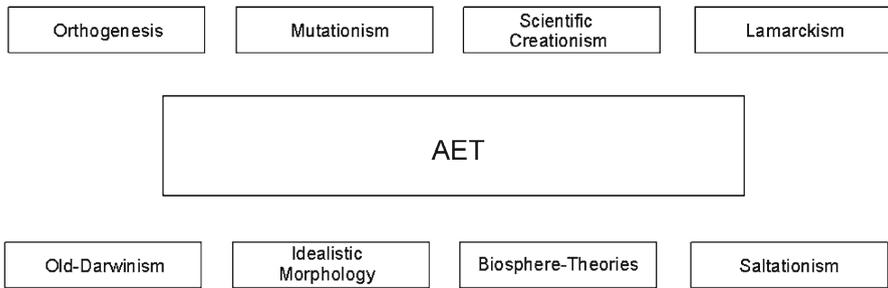posed a comprehensible and coherent model of evolution based on the selected aspects

Orthogenesis	Mutationism	Scientific Creationism	Lamarckism

AET

Old-Darwinism	Idealistic Morphology	Biosphere-Theories	Saltationism

Fig. 1 Alternative evolutionary theories (AET) in the 20th century: An overview

of Darwin's initial theory. The proposed model included three crucial assumptions: (1) natural selection is the only direction-giving factor; (2) random mutation and recombination causes variation and therefore implies the incorporation of genetics into the theory; (3) geographic isolation is the most important mechanism separating populations (Junker 2004). The original 'Origin-Of-Species-Darwinism' served the STE as an argumentative model and paradigmatic framework, but did not coincide with the newly-established theoretical system. Thus it was the 'architects' of the STE, who first drew an ultimate and clearly definable line between 'Darwinism' and his actual and potential alternatives. Mainstream Darwinism constituted itself in the form of the STE from the retrospective reading of Darwin's works. Briefly stated, Darwinism was defined by Ernst Mayr (1904–2005) as 'the theory that selection is the only direction-giving factor in evolution' (Mayr 1980, p. 3).

The STE has not only enriched itself by forming an alliance with genetics, but also restricted the panoply of even potentially acceptable approaches. For example, the concept of the inheritance of acquired characters was declared as incompatible with Darwinism, although Darwin himself explicitly committed to 'a limited amount' of this Lamarckian mechanism (Bowler 2003, p. 160). To designate these developments, the term 'Second Darwinian Revolution' was coined (e.g., Junker and Hoßfeld 2001). Since the categorization of alternative concepts depends on the self-awareness and historical development of Darwinism, the term 'Alternative Evolutionary Theories' is coined here to describe all theories which (1) explicitly understood/understand themselves as alternatives to one of the historical forms of Darwinism; (2) appear in the retrospective view of the STE as inconsistent with the Darwinian view on evolution, and (3) are interpreted by the supporters of the contemporary mainstream Darwinism as competing approaches.

In the following sections, we outline eight well articulated ATE (see Fig. 1) trying to give a broad international perspective. These theories represent coherent and relatively independent argumentative constructions. One should, however, note, that the concepts we describe below as solitary theoretical entities, in the majority of cases appear in the real history of science as elements of more complex theoretical systems. Furthermore, the actual historical incarnations of these ideas often deviated from their pure form, because of individual, social–cultural, and other reasons. We illustrate each ATE by historical case studies. Our examples are predominantly theories of the 'blooming time' of ATE (approximately 1st third of the 20th century) and taken predominantly

from the German language countries, since German resistance to the Synthesis was especially strong, well articulated and very influential even during the so called time of 'post-Synthesis' (according to Mayr, a period approximately after 1947).[1]

Our overview has the objective of making our study relevant to bioeconomists. The need for the 'alternatives' to the STE in social-economic studies was substantiated, for example, by Colombatto (2003), who maintains that the natural-selection theory is 'ill suited' to describing evolutionary processes in economics. He proposed an alternative 'non-Darwinian' approach by equating the 'non-Darwinian' approach with a definite version of neo-Lamarckism. Yet, as we will show, there is a palette of alternative approaches within and beyond the neo-Lamarckism. We hope to give bioeconomists more choice in their theoretical modeling and constructing of analogies between biology and economics. It will also be shown that in the light of suggested definitions the concept of 'universal Darwinism' recently discussed in bioeconomics makes little sense as a generalizing category. In addition, in the concluding part of the paper we demonstrate that the majority of alternative approaches are far from being pigeonholed as archaic and once and for all wiped off the theoretical landscape. On the contrary, in recent years one can observe some renascent interest in the theoretical 'heresies'.

2 Saltationism

The advocates of saltationism deny the Darwinian idea of slowly and gradually growing divergence of character as the only source of evolutionary progress. They would not necessarily completely deny gradual variation, but claim that cardinally new 'body plans' come into being as a result of saltations (sudden, discontinuous and crucial changes, for example, the series of macromutations). The latter are responsible for the sudden appearance of new higher taxa including classes and orders, while small variation is supposed to be responsible for the fine adaptations below the species level.

One of the advocates of evolution by means of discontinuous sports was the British scholar William Bateson (1861–1926) known, among other things, as the inventor of the term 'genetics'. For Bateson evolution not only discontinuously proceeded, but was also an 'unfolding of certain potentials' (Bowler 1983, p. 185). The German-American geneticist Richard Goldschmidt (1878–1958) developed a theory of discontinuous evolution, which claimed that 'species and the higher categories originate in single macroevolutionary steps as completely new genetic systems' (Goldschmidt 1940, p. 396). Well articulated theories of random saltation were developed by the German paleontologists Karl Beurlen (1901–1985) and Otto Heinrich Schindewolf (1896–1971). Beurlen declared that Darwinian gradualism contradicts the empirical data of paleontology and claimed that 'paleontological findings [. . .] unambiguously show saltations' (Beurlen 1930, p. 537). He based his argument on the comparative-morphological description of, for example, different classes of molluscs combined with the idea of morpho-physiological correlation. Considering different design of their shells the snails, he argued, can be clearly separated in different types. The

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[1] Characteristic in this respect is Mayr's report on the 'Phylogenetic Symposium' in Hamburg (1956), where he presented the basic principles of the Evolutionary Synthesis and where 'all those attending (with exception of the geneticist de Lattin) argued against the Synthesis' (Mayr 1999).

anatomy of the soft bodies in each type correlates perfectly with the design of the shells, their mantles and mantle cavities making no sense in the absence of shell. All these correlated features make sense only as a whole and could not appear gradually. Thus, molluscs, Beurlen concluded, could be only a result of saltations, which are undirected, random, non-Lamarckian events leading to a 'phylogenetic explosion'. Beurlen's theory strongly influenced Schindewolf, who developed one of the most influential saltationist theories.

2.1 The theory of 'typostrophe' after Otto H. Schindewolf

Schindewolf was the most influential paleontologist in post-war Germany and his theory of evolutionary change dominated German paleontology (Reif 1993). He was a pupil of Rudolf Wedekind (1883–1961), who pioneered the use of statistical methods in paleontology. In 1933 he became director of the Prussian Geological Institute. After the Second World War Schindewolf for a short time acted as paleontology Professor at the Humboldt University in Berlin (1947). A year later he was given a Chair in Geology and Paleontology at Tübingen University, which he held until 1964. He died in 1971, and was active until his last years.

Schindewolf championed a complex theory embracing saltationism, orthogenesis and typology. In Schindewolf's opinion Darwinians pushed paleontology and morphology towards the unsteady ground of transient hypotheses: 'The old morphology[2] was unbiased and free of hypotheses, i.e. it conducted comparative form studies with the greatest possible objectivity. It was the phylogenetic turn which introduced strongly subjective elements into morphology' (Schindewolf 1962, p. 60). Yet systematics, Schindewolf believed, is a domain preserved for morphology. One of Schindewolf's concerns was the applicability Mayr's 'biological' definition of species ('Species are groups of actually (or potentially) interbreeding natural populations which are reproductively isolated from other such groups', Mayer et al. 1953, p. 25) in the praxis of paleontology. Thus, analyzing Mayr's famous species definition Schindewolf (1962, p. 65) claimed that it is hardly applicable to fossil species: 'This definition might be theoretically incontestable, although a serious shortage is that so general species concept excludes all asexually propagating organisms. *But we cannot do anything with it in praxis*; it provides no applicable handle to determining species identity of any given form.' To avoid these difficulties Schindewolf (1962, p. 67) proposed a definition of species that could be applied to classifying fossil remains: 'Species are series of individuals, which coincide in the totality of their typical characters and manifest only minor and fluent variability in the spatially or temporally interfacing [*aneinander anschließenden*] populations.' With this definition he proclaimed the priority of morphological methods in paleontology.

Based on this historical and logical priority of morphology Schindewolf created his theory of 'typostrophy' (Fig. 2). The theory is based on a combination of orthogenetic and saltationist principles as well as on the idea of cyclicity (Reif 1986). Cyclicity in this case means that evolution proceeds by means of a succession of relatively
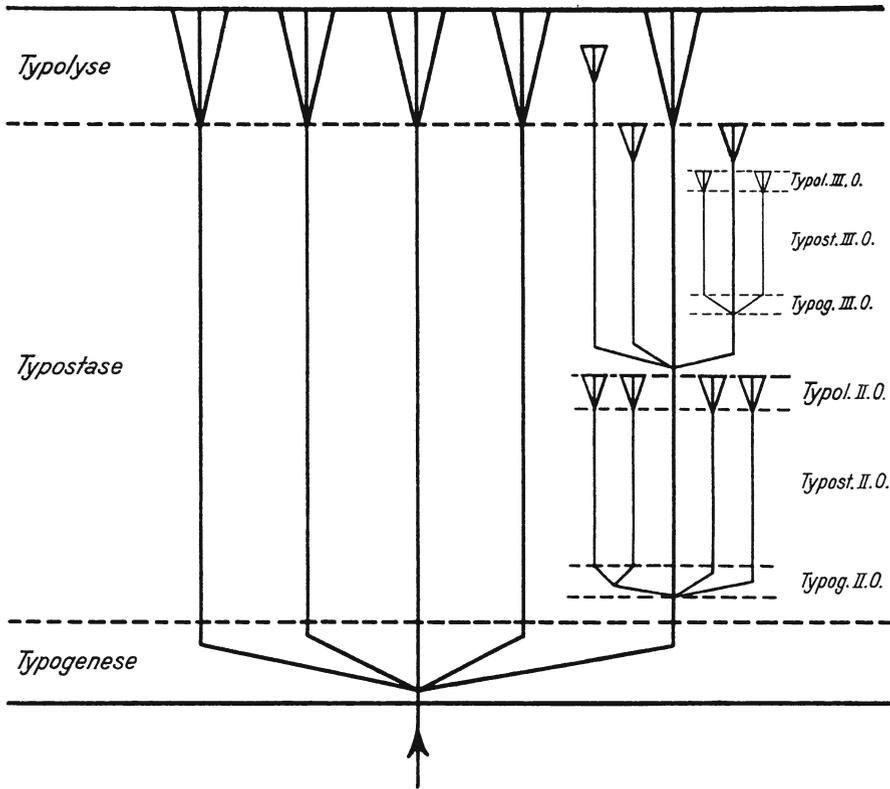
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[2] 'Old' in the sense of pre-Darwinian.

Fig. 2 Schindewolf's view on the evolutionary process as schematically divided into the three phyletic phases: Typogenesis, typostasis and typolysis. In the phase of typogenesis appears a *Bauplan* (body plan) of a new clade, which immediately splits up into subtypes, which then remain unchanged during the whole typostasis. In the following short phase of typolysis the subtypes lose their self-identity and undergo degenerative split-ups (from: Schindewolf 1964, p. 89)

autonomous cycles. Within a certain cycle several morphological forms replace each other in the course of time, representing various stages of development of a certain type (Schindewolf 1956). Schindewolf divided evolutionary development into three successive stages, which differed in both velocity and other important characteristics: typogenesis, typostasis, and typolysis. *Typogenesis* is a sudden, undirected and explosion-like appearance of a new type (usually a new order or even class) due to rapid and random alterations in very early stages of ontogenesis, which then—in the course of generations—lead to changes in the adult stages. Schindewolf called this process 'proterogenesis' (Schindewolf 1936, pp. 26, 101). Schindewolf emphasised that in contrast to Darwinian gradualism this view is very close to a simple description of what can be 'really' seen in the fossil records. The 'unfolding' of a type is a directed, irreversible process. This process is independent of the local environment and governed by the internal potency of the type in question (Schindewolf 1947, p. 370). Thus evolution is regarded as an autonomous process. New types occur through parallel deviation in numerous individuals. According to Schindewolf, neither Lamarckian nor Darwinian

explanations could suffice for understanding the evolutionary process. The typogenetic 'explosion' can be due to physical or chemical conditions in the environment leading to a radical escalation of mutability in a certain group of organisms (Schindewolf 1936, p. 93). Schindewolf speculated about the possible internal mechanisms of mutations and favored Richard Goldschmidt's theory of macromutations ('hopeful monsters'). However, this concept has only a secondary role in Schindewolf's own theory and he abandoned Goldschmidt's hypothesis in later publications (Schindewolf 1969, p. 10). *Typostasis* is the second stage, which is characterized by slow progressive development of a new type driven by natural selection, which Schindewolf degraded to a subsidiary evolutionary mechanism (Rensch 1980) responsible for the occurrence of minor adaptations in the body plans and operating in the frames of the morphogenetic constraints. Due to these constraints the type's evolution in the phase of typostasis proceeds orthogenetically, although Schindewolf excluded all finalistic and mystic explanations of orthogenesis (Schindewolf 1950, pp. 319–321). The third phase (*typolysis*) is the decay stage of a type. At this stage the organism becomes over-specialized and this leads to the disintegration of the type. The decay is determined by internal laws and proceeds in a manner analogous to the aging of individuals (Schindewolf 1956).

Schindewolf's theory was of a very descriptive nature, although phrased in exotic terminology. In other words, his typology was based on the practical needs of identification and classification of the fossil remains and his saltationism followed this typologically based classification.

3 Mutationism

The champions of mutationism assumed that gradual variation cannot lead to the origin of new species. While the Darwinian variation is supposed to be copious, random, and small in extent (gradual), (see Gould 2002, p. 141), the mutationists claim that new species arise by means of sports (large-effect mutations) caused by sudden genome modifications (mutations). These mutations are random and able to produce a new species in one sport, so that there is no need for assuming the 'gradual evolution plus natural selection' mechanism. Mutationism can be understood as a historical form of *saltationism*, however, the specificity of mutationism is connected with the specific properties that mutationists postulated for their mutations. In the typical saltationist concepts (as shown above for Beurlen and Schindewolf) saltations are able to produce the higher taxa immediately.[3] Besides, the idea of saltations as it is does not include any constraints on the directionality of mutations and their adaptive or non-adaptive character. Typical mutationists usually restricted themselves to the species level and maintained the idea of undirected mutations thus excluding even a potential possibility of *neo-Lamarckian* (see below) explanations.

As representatives of mutationism one can list the German botanist Carl Correns (1864–1933), the Russian botanist Sergej I. Korshinsky (1861–1900) and the French geneticist Emile Guyénot (1885–1963). The best known mutationist, also regarded

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[3] As Schindewolf metaphorically expressed it based on Walter Garstang (1868–1949): 'The first bird hatched from a reptile egg'.

as the founder of the proper mutationist movement, was the Dutch botanist Hugo de Vries (1848–1935).

3.1 Mutationism after Hugo de Vries

In the history of biology, mutationism is usually associated with the name de Vries. The received view is that de Vries was a crucial figure in the rediscovery of Mendel's laws. However, instead of taking the way of synthesis of genetics and selectionism, de Vries rebelled against the theory of natural selection. In short, on the basis of his experiments with *Oenothera lamarckiana* de Vries proposed that Darwin's gradual variations are nonheritable 'fluctuations', while new species arise only by means of sudden, non-adaptive, fully formed, random (undirected), directly observable and experimentally provable saltations occurring without any transitional forms: 'According to the mutation theory species do not arise due to gradual selection proceeding over hundreds or thousands of years, but occur in stages by means of sudden, even if very small, modifications' (de Vries 1901, p. 150); 'a new species appears therefore in a single step; it arises from a former species without observable prearrangement and without transitions' (Ibid., p. 1). These 'single steps' (mutations) occur simultaneously in a great number of individuals and are responsible for evolutionary significant changes. The species of de Vries survive only as a whole with the entire set of adaptive or non-adaptive characters and the best that natural selection can do is to eliminate absolutely hopeless mutants.

However it must be remarked that the above extraction of de Vries' theory does not perfectly correspond to the exact historical reconstruction of his view, which is of rather sophisticated nature. Thus, recently Gould (2002, pp. 418–446) revolted against the simplification of the de Vries' theory. Gould fights to rescue de Vries from the charge of being indubitably anti-Darwinian, although, he argues, de Vries' own claims on selectionism were very contradictory. De Vries' understanding of Darwinian, selectionist logic was 'clear and subtle', Gould claims, and if we could regard de Vries' speciational steps as relatively small on the geological scale then the Darwinian logic would be still applicable in the mutation theory. It seems to be in accord with de Vries' own views on selection, Gould claims, since he 'denies selection at Darwin's own favored level of organisms in populations, and grants power to Darwin's mechanism only at the higher level of sustained trends among species' (Gould 2002, p. 444). In other words, de Vries' rejection of selectionism on the microevolutionary level does not automatically lead to the anti-selectionism also on the macroevolutionary level as well.

4 Neo-Lamarckism

Apart from the debates on the genuine nature of Lamarck's original theory, the term Lamarckism (neo-Lamarckism) 'has come to mean the inheritance of acquired characteristics' (Bowler 2003, p. 90). Based on this principle, neo-Lamarckians explain the high rate of evolutionary change and the appearance of complex adaptive structures thus avoiding difficulties connected with assuming 'chancy', Darwinian variation.

The concept of inheritance of acquired characters violates one of the most crucial assumptions of Darwinism, which claims that variation is random, i.e., non-adaptive. Many of the 20th century Lamarckians did not reject natural selection completely and combined the inheritance of acquired characteristics with the Darwinian idea of natural selection. Influential representatives of neo-Lamarckism were, for example, the Austrian palaeontologist Othenio Abel (1875–1946), the German biologist Paul Kammerer (1880–1928), the American palaeontologist Edward D. Cope (1840–1897), and the pioneer of experimental physiology in Sweden Nils Holmgren (1877–1897),[4] as well as the German anatomist and zoologist Hans Böker (1886–1939). Neo-Lamarckian theories became especially wide spread in France in the early 20th century (e.g., Le Dantec 1909; Rabaud 1921). Their predominance in the French theoretical landscape was so strong that it allowed Alphonse Labbé to claim that Darwinism should be qualified as a specifically British scientific project alien to nations with other 'directionalities of mind' (Labbé 1937, p. 45). French neo-Lamarckians saw mutationists (e.g., Guyénot 1921) as well as neo-Darwinians (August Weismann) as their major opponents.

Yet the Lamarckians never represented a theoretical monolith, and the idea of the inheritance of acquired characteristics must be rather seen as a kind of 'umbrella-concept' for several evolutionary mechanisms. The differences occur in answering questions of how the heritable features can be acquired and what is the exact mechanism of inheritance. There are as a minimum two major neo-Lamarckian approaches to these issues. The first approach developed by Lamarck himself and advocated, for example by Cope, proceeded from the so called use/disuse + inheritance concept claiming that an organ adapts or loses his adaptive value following its actual involvement into everyday functioning (favorite example: the blindness of cave animals). The second approach, represented, for instance, by the German botanist Carl von Nägeli (1817–1891) advocated the idea of 'direct environmental impact'[5] [*Theorie der direkten Bewirkung*] on the organism's heredity Nägeli 1884, p. 291). The 'direct inheritance' induced variation, which may not be necessarily or completely adaptive and therefore the champions of this direct environmentally induced inheritance often advocated *orthogenesis* (see below) as well, being hostile to the use/disuse theorists.

A distinct and strongly ideologically affected version of neo-Lamarckism was developed in the 1930–1950s by the Soviet agronomist Trofim D. Lysenko (1898–1976) and became known as Lysenkoism, which was later also imported into the GDR (East Germany) and enjoyed significant influence (Hoßfeld and Olsson 2002). Lysenkoists, as well as many 19th century Lamarckians, attributed inheritance to the whole organism and denied the existence of discrete hereditary factors like genes. Correspondingly, they believed that the changing environment can directly induce novel features. For example, Lysenko believed that winter varieties of wheat, which normally require a period of cold treatment, can be changed into spring forms without cold treatment.[6] Such a ludicrous form of Lamarckism could not survive in the

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[4] The resistance to Darwinism in Sweden was remarkably strong and persistent. Details in: Olsson (2005).

[5] This approach is also known as Geoffroyism (after E. Geoffroy Saint-Hilaire, 1772–1844).

[6] In other words, he claimed that winter crops can be directly transformed into spring crops.

20th century without support of extreme totalitarian regimes. Therefore Lysenkoism weakened after Stalin's death in 1953, but lost influence only after the retirement of Nikita Khrushchev in 1964.

4.1 Neo-Lamarckism after Hans Böker

In 1924 Böker wrote a Paper *Begründung einer biologischen Morphologie* (Foundations of biological morphology), where he declared his Lamarckian research program by stating that species 'vary before our very eyes by means of inheritance of acquired features' (Böker 1924, p. 20).

Böker, like many biologists at his time, believed he could create a new biological synthesis in order to describe evolutionary mechanisms properly. He was aware of the mutationist and selectionist research programs but maintained that they were unable to deliver the whole truth: 'If somebody nevertheless claims that he can explain the origin and transformation of species alone by mutation and selection, he may only assure himself of the richness and complexity of anatomical and biological interconnections and coherencies going into the finest details. He would than probably understand that the biomorphological correlations of life cannot be explained alone by separate "features" and "properties" on which a heredity[7] researcher set so much value' (Böker 1937, p. iv).

Böker was opposed to the search for 'separate features' and proposed the holistic research program combining idealistic morphology, genetics, evolutionary morphology (Lamarckian version), functional explanations, ecology and even ethology (Hoßfeld 2002, p. 159). He called his teaching 'comparative biological anatomy' and proceeded from the assumption that the organism is a kind of 'construction' that consists of parts, while being confronted with its environment as a whole. Organisms remain in a harmony with their environment until the former changes. If it happens, then there are two possible pathways for an organism to react on the environmental perturbations: it will either die out or else adapt to the new situation. Adaptation proceeds by means of anatomical re-construction [*Umkonstruktion*] of the whole organism or its parts and these reconstructions are heritable. For that matter it is important to emphasize that not all anatomical structures are 'constructions' for Böker: 'An organism consists of anatomical constructions and indifferent anatomical features; each anatomical construction is representative of a corresponding manifestation of life and environmental conditions' (Böker 1935, p. 9). Considering that 'manifestations of life' are causally determined by the environment, there are causal connections between organisms and their environments. Accordingly, it was essential for Böker's 'comparative biological anatomy' to compare all organisms related to a certain function, i.e. both homologous and analogous. For instance, in studying bats one should compare them with all flying mammals, birds, reptiles and so on. Doing so, one can reconstruct the complete phylogenetic history taking into account ecological, ethological and morphological factors and proceeding from the notion of a biological type

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[7] 'Heredity researcher' means here geneticist.

as it is known from idealistic morphology (see below). The goal of this study was the establishment of regularities or laws observable in the history of organisms.

5 Orthogenesis

The term orthogenesis was coined by a student of Haeckel, German zoologist Wilhelm Haacke (1855–1912) in his book *Gestaltung und Vererbung* (1893). In his views orthogenesis is a concept of constrained variation as opposed to the claim of Darwinism[8] that natural selection selects from the very copious or even inexhaustible material of variation. Accordingly orthogenetic evolution proceeds 'only in a certain direction within each phylogenetic line; orthogenesis is a universal phenomenon' (Haacke 1893, p. 32). At the same time, he distinguished orthogenesis from 'epimorphism', a concept claiming that evolution goes in the direction of increasing perfection of organisms, i.e., from the idea of biological progress. Haacke based his theory on the ideas of several predecessors including the German botanist Carl von Nägeli (1817–1891) and the Swiss-German zoologist Theodor Eimer (1843–1898). In the later works Eimer (1897) adapted the term orthogenesis and succeeded in popularizing this concept (Bowler 1983, p. 150).

In the first half of the 20th century the idea of directed evolution became especially popular and included more then twenty various theories (Popov 2003). Although some of these theories included finalistic ideas (Mayr 1982, p. 959), the common denominator of all of them was the idea of constraints (morphological, molecular etc.), which direct phylogenetic lines in such a way that it makes the mechanism of natural selection superfluous either for the whole evolution or for certain (short or long) periods of phylogenetic history. The majority of advocates of directed evolution proceeded from the assumption that organisms are predisposed to vary in certain directions and this very bias determines major transitions in evolution. They were convinced that these directions are empirically observable in the paleontological record and clearly definable (Fig. 3). Accordingly it was assumed that evolutionary events follow certain clearly definable laws and restrictions and that evolution can proceed significantly or predominantly in a non-adaptive way. In other words, orthogenesis was strongly coupled with the idea of non-adaptive trends in evolution. Various scientists developed orthogenetic ideas, but coined their own terminology. In that way appeared *aristogenesis* of the American paleontologist Henry F. Osborn (1857–1935), *apogenesis* of the Austrian zoologist Hans Przibram (1874–1944), the *Trägheitsgesetz* (the law of inertia) of Othenio Abel, *ologenesi* (hologenesis) of the Italian zoologist Daniele de

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[8] Haacke opposed his views primarily to the neo-Darwinism. Darwin himself was not so categorical in denying any form of constraints. Consider the following quotation: 'The foregoing discussion naturally leads to the question, what is the limit to the possible amount of variation in any part or quality, and, consequently, is there any limit to what selection can effect? Will a racehorse ever be reared fleeter than Eclipse? Can our prize-cattle and sheep be still further improved? Will a gooseberry ever weigh more than that produced by 'London' in 1852? Will the beet-root in France yield a greater percentage of sugar? Will future varieties of wheat and other grain produce heavier crops than our present varieties? These questions cannot be positively answered; but it is certain that we ought to be cautious in answering them by a negative' (Darwin 1883, p. 228).
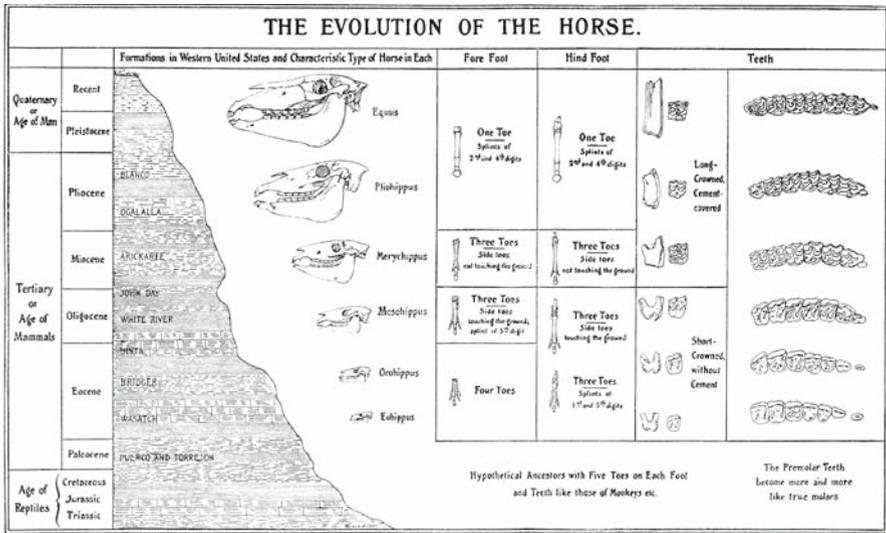
THE EVOLUTION OF THE HORSE.

Fig. 3 Othenio Abel's example for empirical evidences in favor of linear evolution of horses (initially drawn by W. D. Matthew (1871–1930), from Abel 1928, p. 35)

Rosa (1857–1944), *nomogenesis* of the Russian biologist and geographer Lew (Leo) S. Berg (1876–1950) and many others.

5.1 Nomogenesis after Lew S. Berg

The nomogenesis-theory was developed in the early 1920s by Lew Berg. His book *Nomogenesis* was first published in Russian (1922) and later translated into English (Berg 1926 [reissued 1969]). The theory was based on the huge amount of empirical data and offered very consequent and strong criticism of the Darwinian evolutionary theory (Levit and Hoßfeld 2005).

The theory suggests a number of logically relatively independent claims. The most basic assertion is that evolution is a directed process: 'Darwin believed that characters vary in all directions, like, let us say, rays issuing from the sun. [. . .] We, on the contrary, claim that variation of characters is confined within certain limits, that it follows a definite course, like an electric current moving along a wire' (Berg 1969, p. 158).

The limits Berg talks about are supposed to be determined by both internal and external factors. The internal factors are reflected by the term *autonomic orthogenesis* (Berg 1969, p. 114) and express themselves, for example, in the fact that the organisms often evolve contrary to the environmental changes. The latter can be exemplified by the cases of the species' extinctions. The external factors mean the impact of the geographical landscape on evolutionary process. The landscape affects a species 'in an imperative manner' by the entire combinations of elements constituting this landscape so far as the organization of species permits variation in a determined direction (Berg 1969, p. 265).

In effect, evolution actually follows a middle course determined by the internal and external factors. Such double limitation of the variability, Berg argues, does not leave much space for natural selection, a fact also supported by paleontological records, because all phylogenetic branches look more or less like straight lines. To explain evolution in the absence of natural selection, Berg proposed the concept of the directed mass-mutations. Following Wilhelm Waagen (1841–1900), he labeled them *Waagen-mutations*: 'New species arise by means of a mass transformation of a great number of individuals, which happens due to Waagen mutations [. . .]. This mass transformation is a phenomenon of geological order. It is connected with the alteration of fauna of a certain horizon and comes about in certain periods to cease then for a long time' (Berg 1977, p. 317). Thus, evolution proceeds essentially by mass-mutations, which are canalized by external and internal factors, in such a way that a new species occurs with a high probability being almost perfectly adapted. A newly occurred species then begets the subordinate taxonomic categories, which appear to be perfectly adapted to their environments. 'Adaptation' in this context means incorporation into a specific landscape. At the same time the evolution of species is cyclic and includes non-adaptive trends similar to the life cycle of individual organisms: 'Every group of organisms in the course of a definite period attains its optimum, after which, obeying certain internal impulses concealed in the constitution of the organism, it becomes extinct or is relegated to a secondary position, yielding its place to others' (Berg 1969, p. 70).

6 Old-Darwinism

'Old-Darwinism' is a German theoretical movement, which was represented mainly by the influential Jena biologists Ernst Haeckel (1834–1919) and Ludwig H. Plate (1862–1937) (cf. Tort 1996; Riedl 2003, p. 89; Levit and Hoßfeld 2006). Even from the contemporary view, old-Darwinism in its fully established and explicit form (Plate) cannot be reduced to any other theoretical school. The specificity of this theory lay in an attempt to combine the standard Darwinian factors of evolution (mutation, recombination, geographic isolation, natural selection) with the neo-Lamarckian and orthogenetic mechanisms and to define the exact role of all these mechanisms in evolutionary process. Old-Darwinians legitimately insisted that they exactly follow the initial ideas of Darwin, who assumed Lamarckian mechanisms and the idea of constraints as auxiliary hypotheses as well.

6.1 Old-Darwinism after Ludwig Plate

Plate proposed a concept combining all valuable theoretical movements and new disciplines of the biology of his time. He developed a research program which he called 'old-Darwinism' during more then thirty years of experimental and theoretical investigations (e.g., Plate 1913, 1932–1938). In addition to Darwin and himself, Plate counts Ernst Haeckel, Richard Semon (1859–1919), Wilhelm Roux (1850–1924), Richard Hertwig, Fritz v. Wettstein (1895–1945), Berthold Hatschek (1854–1941), Jan Paulus Lotsy (1867–1941), Franz Weidenreich (1873–1948) and even the future 'co-architect'

of the evolutionary synthesis Bernhard Rensch among the old-Darwinians (1900–1990). According to Plate, old-Darwinism follows exactly the initial ideas of Darwin while at the same time adapting and processing all healthy and empirically verifiable scientific achievements. Plate aimed to combine all fruitful theoretical approaches (Lamarckism, selectionism, orthogenesis) with the most innovative field of the experimental biology like genetics. The core of Plate's evolutionary theory can be grasped into two theses:

– 'Darwinism is a 'stochastic-theory' taking into account variations occurring by chance in the individuals of a certain species' (Plate 1913, p. 222).
– 'However the harmonic modification of various features is more easily conceivable from the Lamarckian standpoint' (Plate 1913, p. 224).

In Plate's later works (Plate 1932–1938) we find all the basic factors of evolution later adapted by the Evolutionary Synthesis. Thus Plate claimed that random mutations and recombinations deliver the bulk of raw material of evolution. Natural selection and geographical isolation perform a major role in evolution (Plate 1933, p. 1045). Also what is now known as 'population thinking' is of great importance for Plate and he analyses the 'laws of populations' with some mathematics (Plate 1933, pp. 1047–1052). Yet Plate also allows also other evolutionary mechanisms going beyond the STE. So Plate accepts both macro- and directed-mutations, orthogenetic restrictions and the inheritance of acquired characters. In a monograph, exceeding 2000 pages, Plate investigated into the problem how all these mechanisms can co-exist in evolution. It is, however, important to stress that the neo-Lamarckian machinery in Plate's mature works differs from that of many other neo-Lamarckians (see above). The 'inheritance of the acquired properties' is conceivable only in the course of many generations and only in the frame of a population exposed to a specific environmental influence. New characters, Plate argues, appear as a response to certain continuous stimuli on cytoplasm. Lamarckian heredity, Plate underlines, coexists in nature with 'Mendelian' random mutations.

7 Idealistic morphology

Idealistic morphology was (and is) not a coherent theory, but rather a theoretical movement most influential in the German-speaking countries, which embraced, however, several characteristic methodological postulates and also included specific theoretical elements non-reducible to any other theoretical systems.

As a first historical approximation one can define idealistic morphology as a heterogeneous methodological program intended to revive the idea of type in the way how it was used by Johann W. von Goethe (1749–1832). Idealistic morphology as the supreme historical manifestation of typology—an empirically based methodology—declared a primacy of structure over function and claimed that organisms are structural phenomena to be ordered in logical schemes (cf. Reif 1998). The cornerstone of typology was the concept of type as an abstract pattern representing a certain class of phenomena and embodying the norm of this class. The primary objective of the pure typology was creating not necessarily phylogenetic classification systems

for living natural bodies based on the structurally explicable characters. The practical method of doing it was comparative-morphological studies. Idealistic morphologists following the typological assessment looked for homologies presupposing that two characters of two different taxa are homologous, because they represent an identical structural design. Typology as non-phylogenetic foundation of the idealistic morphology was conceptually neutral in respect to any hypothesis of evolutionary mechanisms. This means, that idealistic morphology can be represented as a two-step-methodology (typology + auxiliary concepts). In other words, idealistic-morphological theories consisted of typological methodology accompanied by other methodological elements, such as Lamarckism, saltationism, creationism, mutationism, orthogenesis and natural selection mixed into a unique theoretical structure (Levit and Meister 2006). The characteristic feature of idealistic morphology was also a kind of neo-platonic metaphysics, which was incorporated in several (but not to all) idealistic-morphological theoretical systems.

Many influential German-speaking scientists practiced idealistic morphology: for example the zoologist Adolf Naef (1883–1949) (Breidbach 2003), the anatomist Wilhelm Lubosch (1875–1938), the palaeontologist Edgar Dacqué (1878–1945) (Meister 2005a) and the botanist Wilhelm Troll (1897–1978) (Meister 2005b).

7.1 Idealistic morphology after Wilhelm Troll

Even at the beginning of his scientific career Troll appeared to be strongly influenced by the typological morphology of Goethe. Troll (1925) wrote a programmatic paper, where he explicitly credited his understanding of morphology to Goethe and sharply contrasted Goethe's views with those of Immanuel Kant (1724–1804). He proceeded from the assumption that there are two modes of cognition: (1) A 'discursive-analytical ability' [*diskursives analytisches Vermögen*] as articulated by Kant and (2) an intuitive ability or 'viewing judgment' [*anschauende Urteilskraft*] as represented by Goethe (Troll 1925, pp. 540–541; Goethe 1932, pp. 289–290). The discursive-analytical ability is useful in sciences such as physics, but fails in morphology because 'an organism opposes a certain independence to the causal events and controls them more than it is controlled itself'. The comprehension of living phenomena as 'individuals' is possible only by combining the intuitive and holistic approaches with the platonic concept of 'cognition as reminiscence', which Troll termed 'cognition as resonance'. This intuitive, imaginative mode of cognition is truly essential for scientific morphology founded by Goethe, while the Kantian analytical way expresses itself in genetics and the theory of natural selection (Troll 1925, p. 565). However, morphology is an empirical science and, in full accordance with Goethe (and partially with Plato), the imaginative power alone cannot lead to significant advances in morphology. Imagination must be supported by empirical studies. Measuring and comparing various plant characters in order to find common traits in the diversity of forms allowed Troll to construct the 'circles of types' [*Typenkreise*] defining frontiers and modifications of certain types (Fig. 4). The types reconstructed by this way have morphological eigenvalue and concentrate on analogy as contrasted to homology important for studies of phylogeny (Troll 1928, p. VII). According to Troll, the discovered structural
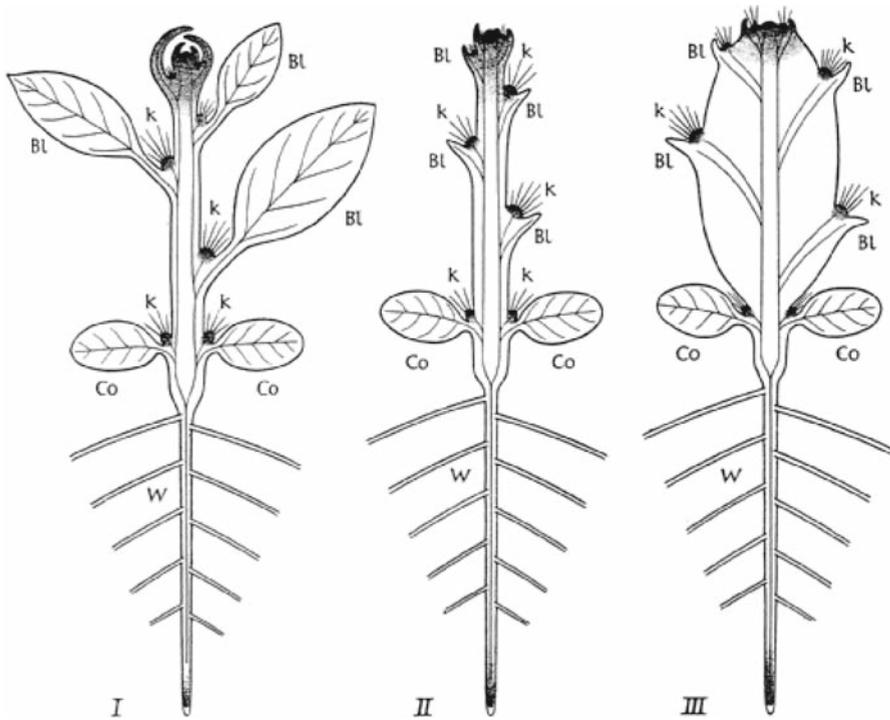
Fig. 4 Troll's scheme of the origins of the cactus type. *W*—primary roots; *Bl*—leaves or their rudiments; *k*—thorny lateral buds (From: Troll 1951, p. 383)

laws are not simple generalizations or abstractions but reveal regularities existing objectively, 'in reality' and practically applicable (for example, for predicting forms, which can exist in principle). The 'ideas' of idealistic morphology, Troll thus argued, are not creations of somebody's voluntary imagination, and in that sense Troll used the predicate *platonic* to designate the 'objectively' existing ideas of types. Finally Troll postulated the existence of an immanent formatting principle purposefully creating perfectly adapted organismic plans [*Organismenplan*]. The peculiarity of living being is determined by 'the thoughts and ideas of a creative power that penetrate nature, acting from the world's background [. . .] and bringing into being the new type-like basic organic forms' (Troll 1937, p. VI). In one of his last published papers he made his views even more explicit: 'God displays himself proportionately in the universal-natural phenomena, which reflect in this way [his status] as a completely transcendent entity [*andersartige Wesenheit*]' (Troll 1952, p. 13).

8 The Biosphere theory and the global approach

Although the rudiments of the biosphere concept can be found already in Plato's *Timaeus* and in modern times are to be found in James Hutton's (1726–1797) 'super-organism' or Lorenz Oken's (1779–1851) *Weltorganismus* (Breidbach and Ghiselin

2002), the first scientist to use the term 'biosphere' in the modern sense was the Austrian geologist Eduard Suess (1831–1914). The first scientific theory of the biosphere was systematically presented in V. I. Vernadsky's (1863–1945) book *The Biosphere* (1926). Comparable global approaches were also developed by the French palaeontologist and Jesuit Father P. Teilhard de Chardin (1881–1955), and Russian morphologist Vladimir N. Beklemishev (1890–1962). At present, various versions of the theory are supported by the Russian microbiologist Georgii A. Zavarzin (e.g., Zavarzin 1997, 2003), the English inventor James Lovelock and the American microbiologist Lynn Margulis (e.g., Lovelock 1986, 1996; Lovelock and Margulis 1974; Margulis 1996) and the German geomicrobiologist Wolfgang E. Krumbein (Krumbein and Schellnhuber 1992).

The idea in its most general form interprets the Biosphere (the total sum of living organisms with their environment) as a dynamic, self-regulating system evolving in accord with the own laws. In the most articulated contemporary version, represented—in our view—by Zavarzin (1997, 2003), the theory claims that phylogenetically independent prokaryotes are basic for the running of biogeochemical cycles of the biosphere. This implies that (1) the strict monophyletism propagated by the STE cannot be applied to the early stages of the biospheric evolution; (2) evolution has an additive character ('new' + 'old' and not 'new' instead of 'old'); and (3) the Biosphere functions as a well-balanced system of functionally complementary organisms and the Darwinian laws work only on the lowest level of this system.

The global theories can, to a certain extent, co-exist 'peacefully' with Darwinism. They come into conflict with it only so far they constrain the monopoly of natural selection as the only 'direction-giving' factor in evolution and challenge the consistent monophyletism throughout the whole history of the biosphere.

8.1 The biosphere theory after V. I. Vernadsky

Vladimir Ivanovich Vernadsky was one of the greatest Russian naturalists. He is regarded as one of the founders of modern geochemistry, biogeochemistry, and a pioneer of radiogeology (Levit 2001). He is also regarded as a pioneer of genetic mineralogy and one of the outstanding crystallographers.

In the theoretical system of Vernadsky, the concept of the biosphere is included in a new branch of science created by him: *biogeochemistry*. Biogeochemistry studies the geological manifestations of life and considers biochemical processes in living organisms in relation to their impact on the geosphere (Vernadsky 1997, p. 156): 'The competence of biogeochemistry is defined, on the one hand, by the geological manifestations of life taking place under this aspect, and on the other, by the internal biochemical processes in the organisms—the living population of our planet. In both cases (for biogeochemistry is a part of geochemistry) one may identify as the study of objects not only chemical elements, i.e., the usual mixtures of isotopes, but also various isotopes of one and the same chemical element'. Neither living organisms by themselves nor their environment abstracted from them are, Vernadsky argued, the specific objects of biogeochemistry. A biogeochemist is interested, first of all, in studying the cyclic processes of the exchange of chemical elements between living

organisms and their environment. In order to define this specific geological domain as the research field of the newly created science, biogeochemistry, Vernadsky introduced his concept of the *biosphere*. The biosphere of the Earth appears as a geosphere occupied and organized by life and thus can be seen as a geological envelope.

Examining living matter from the biogeochemical viewpoint, Vernadsky (1994) arrived at the conclusion that the chemical compounds of the different species do not reflect the chemical composition of their environment, but, on the contrary, living matter has determined the geochemical history of almost all elements of the Earth's crust in the process of making the environment favorable to itself. Thus, living matter shapes the biosphere into a self-regulating system. The structure of the biosphere is described as a dynamic equilibrium: 'Not a single point of this system is fixed during the course of geological time. All points oscillate around a certain midpoint' (Vernadsky 1997, pp. 225–227).

A good example of such dynamic equilibrium is the troposphere. Vernadsky claimed (1965, p. 238) that 'all basic gases of the troposphere and of the higher gaseous envelopes—N_2, O_2, CO_2, H_2S, CH_4, etc.—are produced and quantitatively balanced by the total activity of living matter. Their sum total is quantitatively invariable over geological time...'. Thus, Vernadsky concludes, 'life, i.e. living matter creates the troposphere and constantly maintains it in a specific dynamic equilibrium'. It can be remarked here, that what is known now as the 1st Gaian principle of atmospheric regulation (Lovelock and Margulis 1974) actually was derived by Vernadsky on the basis of his biogeochemical research 50 years before Lovelock. The evolution of the biosphere, Vernadsky claimed, is a directed process. The directedness of evolution is expressed, first of all, in the acceleration of the biogenic migration of atoms: 'According to the second biogeochemical principle, the evolution of a species must move in a certain direction, namely, in the direction of increasing the biogenic migration of atoms. That means that evolution must have a directionality' (Vernadsky 1965, p. 272). Vernadsky saw the second biogeochemical principle as a geochemical version of Darwin's principle of natural selection and believed that in this way the evolution of species turns into the evolution of the biosphere. In the last version this principle sounds as follows: 'The evolution of species (over geological time), tends towards the creation of stable life forms in the biosphere and moves in the direction of increasing biogenic migration of the atoms' (Vernadsky 1965, p. 270).

In sum, Vernadsky saw the process of evolution as a biospheric (global) phenomenon, so that all crucial evolutionary events can be seen as having their specific function in this larger scale process.

9 'Scientific' creationism

The ordinary religious creationism assumes that the whole world and the biological diversity as its part occurred as a result of supernatural activity and thus makes any discussion on natural causes meaningless. 'Scientific creationism', by contrast, incorporates the concept of creation into scientific theories as an auxiliary but unavoidable element of explanation. It is characteristic of this kind of theories that they include elements immune to any kind of scrutiny. The 'scientific creationists' neither negate

evolutionary process as it is, nor completely distrust paleontological data. The supranatural forces are called for help only for the certain 'crucial events' in the phyletic history. Many of contemporary 'scientific creationists' accept Darwinian mechanisms for microevolution, but deny even the potential possibility of causally explaining macroevolution. By doing so, they abandon the most basic presumption of Darwinism that any kind of evolutionary events can be explained in causal terms. Influential representatives of the 'scientific creationism' were the German ornithologist and pastor Otto Kleinschmidt (1870–1945), the botanist Albert Wigand (1812–1886) as well as the zoologist Albert Fleischmann (1862–1942). In the contemporary literature 'scientific creationism' unfortunately enjoys a broad international influence (for critical analysis see: Kutschera 2004).

9.1 The 'Formenkreislehre' after O. Kleinschmidt

At the beginning of the twentieth century German ornithologist Otto Kleinschmidt, being essentially disagreeing with the ideas of Darwin and Haeckel, formulated his concept of the Formenkreislehre (Circles of Forms), which was based mostly on studies on the birds of prey (Baumgart 2000). He declared it as a new theory of descent (Kleinschmidt 1925, p. 2), which however can be coupled with the religious worldview.

A predominantly typological concept of 'circle of form' builds the basis for this theory, which interprets species diversity as a hierarchically organized system of distinct entities (forms). A 'circle of form' approximately corresponds to species, although the 'circles of form' are constant, closed, clearly definable entities and any variation is possible only in the frame of the 'circles'. The fluctuating forms and colors of various individuals in various geographic regions only detract the observer from the true essence of 'circles', while nothing can influence their essence (Kleinschmidt 1909). The circles are created to be as they are. Accordingly Kleinschmidt rejected not only Darwinian monophyletism, but even the very idea of phyletic affinity between different taxa. His argumentative basis was based on the geographic teaching of 'natural races', which he subdivided into 'real genus' [*Formenkreis*], 'race', and 'variety'.

Kleinschmidt's creationistic concept led him not only to the rejection of the Darwinian theory of descent, but also to the negation of the *post*-Mendelian genetics (cf. Rensch 1929). His criticism of the Darwinian principles is one of the most intensive and extensive assaults on the proper evolutionism (Hoßfeld 2000). At the same time, his studies on individual and geographic variation of Palaearctic birds delivered valuable biological data, which seriously contributed to the empirical basis of biological systematics (Haffer 1995). It was even recently stated that if approached eco-functionally Kleinschmidt's 'circles of forms' can be interpreted as functional units and thus described in terms of contemporary science (Baumgart 2000).

10 Conclusions

According to the nature of their conflict with Darwinism the above theories fall into three categories (cf. Ljubistchev 1973):

Contra-Darwinian theories violate the very fundamentals of any form of scientific evolutionism in that they exclude the continual causality in mechanisms of evolution. They owe their categorizations as 'contra-Darwinian' the fact that the majority of these theories saw and see Darwinism as their key opponent. All forms of 'scientific creationism' including its modern versions such as ID as well as neo-platonic elements in the idealistic morphology belong to this category. Contra-Darwinian theories nevertheless cannot be simply excluded from the history of biology, since they performed significant role in the early stages of formatting evolutionary methodology or, better to say, before the explicit and well-reflected (although not necessarily monolithic) methodology of evolutionary studies took shape. This contemporary methodology allows us to show that these theories include irrational references to events (acts of creation, platonic ideas), which cannot be included in any causal chain explicable in any practicable scientific language. That is why we advocate including contra-Darwinian theories in the historical records, but, at the same time, insist on their incompatibility with the contemporary scientific landscape (they are not 'theories' in the received sense). The widespread confusion between contra-Darwinian theories and scientific anti-Darwinism is dangerous, because it equates potentially fruitful hypotheses (as a minimum in form of constructive critics and empirically based arguments) with approaches negating the very foundations of modern science.

Anti-Darwinian theories proceed from the assumption that evolution is a causally driven, natural process and, in this respect, they stay on the same methodological foundations as the Darwinians. Therefore, although anti-Darwinian theories propose alternative evolutionary mechanisms, their conceptual apparatus is comparable with that of Darwinians and can be analyzed in the same terms. For example, whereas Darwinians insist on random variation, the champions of orthogenesis postulate that variation is restricted. However both discuss the same clearly definable and empirically describable phenomena in mutually compatible terms. Orthogenesis, saltationism and neo-Lamarckism are examples of the anti-Darwinian theories.

Non-Darwinian theories propose an additional evolutionary mechanism, which operates parallel to the Darwinian machinery. They conflict with Darwinism only so far they violate its claim for monopoly in explaining the directions of evolution. Here belong the theories interpreting the biosphere as a self-regulating system evolving according to specific laws constraining from above the course of evolution. Another example is theories of 'non-Darwinian evolutionary domains' claiming that certain periods of evolution (for example, very early stages of earthly life) must be discussed in non-Darwinian terms. It is debatable, whether such theories as the theory of endosymbiosis, or one of its historical forms, which initially occurred as an alternative to Darwinism (Levit and Krumbein 2007) can be put into this category.

Every ATE incorporates at least a part of the Darwinian concepts. In the majority of cases, the question is not whether selection, variation, or isolation are factors of evolution, but to what extent these factors determine evolutionary events and on which systemic level they operate. Whether there are evolutionary domains inaccessible for Darwinian explanatory patterns is also a problem.

ATE performed an important role in the history of evolutionary biology and their critical assaults on Darwinism contributed to the sharpening of arguments and self-identification of the contemporary Darwinism. The triumphal procession of the STE

in the 1960–1970s in the majority of science-making countries and in the majority of biology related disciplines (Ghiselin 1969) pushed the alternative theories into the shadow of the dominating paradigm.

More recently, approximately since the 1980s, however, the ideas connected with ATE experienced some come-back. Thus, the idea of orthogenesis reappeared in form of debates around the developmental and evolutionary constraints (e.g., Wimsatt and Schank 1988; McShea 2005). The radical version of this idea was articulated in the Anglo-Saxon world by the so called 'process-structuralists', who attribute to natural selection only a secondary role in evolution (Goodwin 1984). In Germany the Frankfurt-school of 'constructional morphology' represents an extreme version of the concept (Gudo 2001).

The idea of direct impact of environment on the genome, which is connected with neo-Lamarckism, experiences a come-back as well. The recent debates on neo-Lamarckism were stimulated by the rediscovery of adaptive mutations (Cairns et al. 1988) and the debate concerning epigenetic phenomena (Jablonka and Lamb 1998; Balon 2004) and somatic mutations (e.g., Steele et al. 2004).

Goldschmidt's mutationist–saltationist approach also experiences re-evaluation. Apart from Steven J. Gould (1941–2002), who analyzed the macroevolutionary aspect of Goldschmidt's theory (Gould 2002, pp. 451–466), his idea of 'hopeful monsters' has drawn the interest of geneticists. Thus Günter Theißen has recently claimed that 'several lines of evidence suggest that hopeful monsters played an important role during the origin of key innovations and novel body plans by saltational rather than gradual evolution' (Theißen 2006). The saltatory model of ontogeny was proposed, for instance, by Eugene Balon (2001). There were also some recent attempts to reconsider the applicability of typological methods in systematic biology and plant morphology (Williams and Ebach 2005; Harlan 2005).

Whether the newly increased interest to ATE will result in a kind of 'higher synthesis' remains to be uncovered by future history of biology. It is however evident that the historical studies of ATE and the contemporary discussions around them contribute to the better understanding of Darwinism both historically and systematically. In our view the debates around ATE can be useful for the experts in bioeconomics in several ways. First, the better one understands the nature and the boundaries of a certain method in biology, the more successful one can transfer this method to analyzing non-biological realities. Second, there is much less prohibition of using alternative explanatory patterns in economics than in biology (i.e., Colombatto 2003). For example, the social and economic evolution can arguably be analyzed in terms of legal, psychological, resources determined and ideological constraints of such a power that economic units would be forced to evolve orthogenetically.

In addition, the comprehensive definitions of Darwinism and the concepts it opposed to should help in distinguishing syncretic from synthetic movements in biology and bioeconomics. As an example we briefly examine below the logic of concept of 'generalized' or 'universal Darwinism' recently proposed for the analysis of social–economical systems. The concept assumes that generalized Darwinian ideas can be applied to non-biological, as well as biological, evolving systems (Hodgson and Knudson 2004) and that 'some general features of a Darwinian explanation can be common to all levels, wherever the features of variation, selection and

inheritance are present' ([Hodgson 2002](#)). Darwinism in this interpretation appears to be a very inclusive theory: 'Darwinism involves a general theory of the evolution of all open, complex systems. Furthermore, Darwinism involves a basic philosophical commitment to detailed, cumulative, causal explanations. In both these senses, Darwinism applies fully to socio-economic systems' (Ibid.). At the same time it is argued that Darwinism can be reduced to the general principles of variation, inheritance, and selection and therefore that 'social evolution is *both* Lamarckian and Darwinian. Lamarckism and Darwinism are neither opposites, nor even mutually exclusive' (Ibid.).

Without discussing the very problem of applicability of Darwinian principles to the analysis of socio-economic systems, we argue that the term 'Generalized Darwinism' is misleading. There is nothing specifically Darwinian in this concept. Detailed causal explanation based on the empirical data was the declared purpose of all anti- and non- Darwinian theories. The concepts of variation and inheritance, as they are, cannot be automatically ascribed to the specifically Darwinian terminological apparatus. It is the particular nature of variation and inheritance that make them Darwinian. Thus, if, instead of random and copious, we are told about the rare and restricted variations, we know that we are dealing with a kind of orthogenetic concept. Similarly the acceptance of the 'soft' phenotypic inheritance means the commitment to neo-Lamarckism. Anti-Darwinian concepts and Darwinism in their pure logical form are mutually exclusive, because they represent the opposite interpretations of the basic constitutive elements of the evolutionary machinery: e.g., variations cannot be chancy and directed at the same time. The integration of Darwinian and anti-Darwinian mechanisms in the framework of a more inclusive theoretical system cannot be simply declared, and, at present, all known attempts to create such system failed. Therefore we think that 'Generalized Darwinism' is an inappropriate term in the context of purposes declared by its advocates. A more inclusive concept ('universal evolutionism', 'extended synthesis' or alike) would be more appropriate in the context of bioeconomics.

References

Abel, O. (1928). *Das biologische Trägheitsgesetz*. Wien & Leipzig: Emil Haim & Co.

Balon, E. K. (2001). Saltatory ontogeny and the life-history model: Neglected processes and patterns of evolution. *Journal of Bioeconomics, 3*, 1–26.

Balon, E. K. (2004). Evolution by epigenesis: Farewell to Darwinism, neo- and otherwise. *Rivista di Biologia/Biology Forum, 97*, 269–312.

Baumgart, W. (2000). *Blätter aus dem Naumann-Museum, 19*, 94–120.

Berg, L., & Lew S. (1922). *Nomogenez*. Petrograd: GIZ (in Russian).

Berg, L., & Lew, S. (1926). *Nomogenesis or evolution determined by law* (2nd ed.), (1969). Constable, London. Cambridge & London: MIT Press.

Berg, Leo (Lew) S. (1977). *Trudi po teorii evoluzii*. Leningrad: Nauka (in Russian).

Beurlen, K. (1930). *Vergleichende Stammesgeschichte*. Berlin: Borntraeger.

Böker, H. (1924). Begründung einer biologischen Morphologie. *Zeitschrift für Morphologie und Anthropologie, 24*, 1–22.

Böker, H. (1935/1937). *Einführung in die vergleichende biologische Anatomie der Wirbeltiere* (Vols. I, II). Jena: Gustav Fischer Verlag.

Bowler, P. J. (1983). *The eclipse of Darwinism*. Baltimore & London: The John Hopkins University Press.

Bowler, P. J. (1992). *The non-Darwinian revolution*. Baltimore & London: The Johns Hopkins University Press.

Bowler, P. J. (2003). *Evolution: The history of idea*. Berkeley: University of California Press.

Bowler, P. J. (2004). The specter of Darwinism: The popular image of Darwinism in early twentieth-century Britain. In A. Lustig, R. J. Richards, & M. Ruse (Eds.), *Darwinian Heresies* (pp. 48–68). New York: Cambridge University Press.

Breidbach, O. (2003). Post-Haeckelian comparative biology: Adolf Naef's idealistic morphology. *Theory in Biosciences, 122*, 174–193.

Breidbach, O., & Ghiselin, M. T. (2002). Lorenz Oken and Naturphilosophie in Jena, Paris and London. *History and Philosophy of the Life Sciences, 24*, 219–247.

Cairns, J., Overbaugh, J., & Miller, S. (1988). The origin of mutants. *Nature, 335*, 142–145.

Colombatto, E. (2003). Towards a non-Darwinian theory of institutional change. *Journal of Bioeconomics, 5*, 1–25.

Darwin, C. (1859). *The origin of species by means of natural selection or the preservation of favored races in the struggle of life*. London: Murray.

Darwin, C. (1883). *The variation of animals and plants under domestication* (Vol. 2, 2nd ed.). New York: D. Appleton & Co.

de Vries, H. (1901–1903). *Die Mutationstheorie*. Leipzig: Veit.

Eimer, T. (1897). *Orthogenesis der Schmetterlinge. Ein Beweis bestimmt gerichteter Entwickelung und Ohnmacht der natürlichen Zuchtwahl bei der Artbildung*. Leipzig: Verlag von Wilhelm Engelmann.

Ghiselin, M. T. (1969). *The triumph of the Darwinian method*. Berkeley: University of California Press (between others).

Goldschmidt, R. B. (1940). *The material basis of evolution*. New Haven: Yale University Press.

Goodwin, B. C. (1984). Changing from an evolutionary to a generative paradigm in biology. In J. W. Pollard (Ed.), *Evolutionary theory: Paths into the future* (pp. 99–120). Chichester: Wiley.

Gould, S. J. (1977). *Ontogeny and phylogeny*. Cambridge: The Belknap Press of Harvard University Press.

Gould, S. J. (2002). *The structure of evolutionary theory*. Cambridge: The Belknap Press of Harvard University Press.

Gudo, M. (2001). The development of the critical theory of evolution: The scientific career of Wolfgang F. Gutmann. *Theory in Biosciences, 121*(1), 101–137.

Guyénot, E. (1921). Lamarckisme ou mutationnisme. Revue générale des Sciences (pures et appliquées). *Tome, 32*, 598–606.

Haacke, W. (1893). *Gestalt und Vererbung. Eine Entwickelungsmechanik der Organismen*. Leipzig: T.O. Weigel Nachfolger.

Haffer, J. (1995). Die Ornithologen Ernst Hartert und Otto Kleinschmidt: Darwinistische gegenüber typologischen Ansichten zum Artproblem. Mitteilungen des Zoologischen Museums Berlin (Suppl.) 71 *Annalen der Ornithologie, 19*, 3–25.

Harlan, V. (Ed.) (2005). *Wert und Grenzen des Typus in der botanischen Morphologie* (pp. 31–52). Nümbrecht: Martina Galunder Verlag.

Hodgson, G. M. (2002). Darwinism in economics: From analogy to ontology. *Journal of Evolutionary Economics, 12*, 259–281.

Hodgson, G. M., & Knudson, T. (2004). The firm as an interactor: Firms as vehicles for habits and routines. *Journal of Evolutionary Economics, 14*, 281–307.

Hoßfeld, U. (2000). Formenkreislehre versus Darwinsche Abstammungstheorie. Eine weltanschauliche-wissenschaftliche Kontroverse zwischen Otto Kleinschmidt (1870–1954) und Victor Franz (1883–1950). *Anzeiger des Vereins Thüringer Ornithologen, 4*, 1–26.

Hoßfeld, U. (2002). Konstruktion durch Umkonstruktion: Hans Bökers vergleichende biologische Anatomie der Wirbeltiere. *Verhandlungen zur Geschichte und Theorie der Biologie, 9*, 149–169.

Hoßfeld, U., & Olsson, L. (2002). From the modern synthesis to Lysenkoism, and back? *Science, 297*(5578), 55–56.

Jablonka, E., & Lamb, M. J. (1998). Epigenetic inheritance in evolution. *Journal of Evolutionary Morphology, 13*, 159–183.

Junker, T., & Hoßfeld, U. (2001). *Die Entdeckung der Evolution: Eine revolutionäre Theorie und ihre Geschichte*. Darmstadt: Wissenschaftliche Buchgesellschaft.

Junker, T. (2004). *Die zweite darwinsche Revolution: Geschichte des synthetischen Darwinismus in Deutschland, 1924–1950*. Marburg: Basilisken-Presse.

Kleinschmidt, O. (1909). Zum Darwin Jubiläum. *Falco, 5*, 6–8.

Kleinschmidt, O. (1925). Die Formenkreislehre. *Falco, 21*, 1–7.

Krumbein, W. E., & Schellnhuber, H.-J. (1992). Geophysiology of mineral deposits — a model for a biological driving force of global changes through earth history. *Terra Nova, 4*, 351–362.

Kutschera, U. (2004). *Streitpunkt Evolution: Darwinismus und Intelligentes Design*. Münster: LIT-Verlag.

Labbé, A. (1937). *Le conflit transformiste. coll. "Nouvelle collection scientifique"*. Paris: Félix Alcan Éditeur.

Le Dantec, F. (1909). *La crise du transformisme*. Paris: Félix Alcan Éditeur.

Levit, G. S. (2001). *Biogeochemistry, biosphere, noosphere: The growth of the theoretical system of Vladimir Ivanovich Vernadsky (1863–1945)*. Verlag für Wiss. und Bildung, Berlin.

Levit, G. S., & Hoßfeld, U. (2005). Die Nomogenese: Eine Evolutionstheorie jenseits des Darwinismus und Lamarckismus. *Verhandlungen zur Geschichte und Theorie der Biologie, 11*, 367–388.

Levit, G. S., & Hoßfeld, U. (2006). The forgotten "Old Darwinian" synthesis: The evolutionary theory of Ludwig H. Plate (1862–1937). *NTM International Journal of History and Ethics of Natural Sciences, Technology and Medicine, 14*, 9–25.

Levit, G. S., & Krumbein, W. (2007). Zur Diskussion der Symbiogenesetheorie unter sowjetischen Zoologen und Biologietheoretikern der ersten Hälfte des 20 Jh. In A. Geus & E. Höxtermann (Eds.), *Evolution durch Kooperation—Zur Entstehung der Endosymbiose—Theorie in der Zellbiologie* (pp. 477–503). Reprints und Kommentare, Marburg: Basilisken-Presse.

Levit, G. S., & Meister, K. (2006). The history of essentialism vs. Ernst Mayr's "Essentialism Story": A case study of German idealistic morphology. *Theory in Biosciences, 124*(3–4), 281–307.

Ljubistchev, A. A. (1973). Darwinizm i nedarwinizm. *Priroda, 10*, 44–47 (in Russian).

Lovelock, J. (1986). The biosphere. *New Scientist, 1517*, 51.

Lovelock, J. (1996). *The Gaia hypothesis*. In P. Bunyard (Ed.), *Gaia in action* (pp. 15–33). Edinburgh: Floris Books.

Lovelock, J., & Margulis, L. (1974). *Atmospheric homeostasis by and for the biosphere*: The Gaia hypothesis. *Tellus, 26*, 2–10.

Margulis, L. (1996). James Lovelock's Gaia. In P. Bunyard (Ed.), *Gaia in action* (pp. 54–65). Edinburgh: Floris Books.

Mayr, E. (1980). Prologue: Some thoughts on the history of the evolutionary synthesis. In E. Mayr & W. B. Provine (Eds.), *The evolutionary synthesis*. Cambridge & London: Harvard University Press.

Mayr, E. (1982). *The growth of biological thought: Diversity, evolution and inheritance*. Cambridge: The Belknap Press of Harvard University Press.

Mayr, E. (1984). *Die Entwicklung der biologischen Gedankenwelt*. Berlin: Springer.

Mayr, E. (1999). Thoughts on the evolutionary synthesis in Germany. In T. Junker & E.-M. Engels (Eds.), *Die Entstehung der Synthetischen Theorie: Beiträge zur Geschichte der Evolutionsbiologie in Deutschland* (pp. 19–30). Berlin: Verlag für Wiss. und Bildung.

Mayr, E., Linsley, G. E., & Usinger, R. L. (1953). *Methods and principles of systematic zoology*. New York: McGraw Hill.

McShea, D. W. (2005). The evolution of complexity without natural selection, a possible large-scale trend of the fourth kind. *Paleobiology, 31*(2), 146–156.

Meister, K. (2005a). Metaphysische Konsequenz.—Die Idealistische Morphologie Edgar Daqués. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 235*(2), 197–233.

Meister, K. (2005b). Troll, W. (1897–1978)—Tradierung idealistischer Morphologie in den deutschen botanischen Wissenschaften des 20. Jahrhunderts. *History and Philosophy of the Life Sciences, 27*, 221–247.

Nordenskiöld, E. (1928). *The history of biology*. New York: Tudor Publishing.

Nyhart, L. K. (1995). *Biology takes form: Animal morphology and the German universities, 1800–1900*. Chicago: The University of Chicago Press.

Olsson, L. (2005). Alternatives to Darwinism in Sweden: Lamarckism and idealistic morphology, disbelief in mutations and the poverty of selection. *Jahrbuch für Europäische Wissenschaftskultur, 1*, 47–60.

Plate, L. (1913). *Selektionsprinzip und Probleme der Artbildung: Ein Handbuch des Darwinismus. 4. Auflage*. Leipzig & Berlin: Verlag von Wilhelm Engelmann.

Plate, L. (1932/33/38). *Vererbungslehre: Mit besonderer Berücksichtigung der Abstammungslehre und des Menschen. Bd. I: Mendelismus. (1932). Bd. II Sexualität und Allgemeine Probleme. 1933. Bd. III: Spezielle Genetik einiger Nager. 1938*. Jena: Gustav Fischer Verlag.

Popov, I. (2003). The concepts of directed evolution. In G. S. Levit, J. Popov, U. Hoßfeld, L. Olsson, & O. Breidbach (Eds.), *In the shadow of Darwinism: Alternative evolutionary theories in the 20th century* (pp. 26–48). St. Petersburg: Fineday Press (in Russian with English Abstract).

Rabaud, E. (1921). *L'Hérédité. Coll*. Paris: Armand Colin.

Reif, W.-E. (1986). The search for a macroevolutionary theory in German palaeontology. *Journal of the History of Biology, 19*, 79–130.

Reif, W.-E. (1993). Afterword. In O. Schindewolf & W.-E. Reif (Eds.), *Basic questions in palaeontology* (pp. 435–453). Chicago: University Press.

Reif, W.-E. (1998). Adolf Naefs idealistische Morphologie und das Paradigma typologischer Makroevolution. *Verhandlungen der DGGTB, 1*, 411–424.

Rensch, B. (1929). *Das Prinzip geographischer Rassenkreise und das Problem der Artbildung*. Berlin: Bornträger.

Rensch, B. (1980). Historical development of the present synthetic Neo-Darwinism in Germany. In E. Mayrm & W. B. Provine (Eds.), *The evolutionary synthesis* (pp. 284–302, p. 289). Cambridge & London.

Riedl, R. (2003). *Riedls Kulturgeschichte der Evolutionstheorie: Die Helden, ihre Irrungen und Einsichten*. Berlin: Springer.

Schindewolf, O. H. (1936). *Paläontologie, Entwicklungslehre und Genetik. Kritik und Synthese*. Berlin: Bornträger.

Schindewolf, O. H. (1947). *Fragen der Abstammungslehre. Aufsätze u. Reden der senckenbergischen naturforschenden Gesellschaft 1*. Frankfurt: Kramer.

Schindewolf, O. H. (1950). *Grundlagen der Paläontologie*. Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

Schindewolf, O. H. (1956). *Zeugnisse der Vorzeit. Universität Tübingen 45, Reden bei der feierlichen Übergabe des Rektorates zu Beginn des Sommersemesters am 8. Mai 1956*. Tübingen: Mohr.

Schindewolf, O. H. (1962). Neue Systematik. *Palaeontologische Zeitschrift, 36*, 59–78.

Schindewolf, O. H. (1964). Erdgeschichte und Weltgeschichte. *Abh. Akad. Wiss. U. Lit., math.-nat. Kl., 2*, 53–104.

Schindewolf, O. H. (1969). *Über den "Typus" in morphologischer und phylogenetischer Biologie*. Mainz: Akademie der Wissenschaften und der Literatur.

Steele, E. J., Franklin, A., & Blanden, R. V. (2004). Genesis of the strand biased signature in somatic hypermutation of rearranged immunoglobulin variable genes. *Immunology and Cell Biology, 82*, 209–218.

Theißen, G. (2006). The proper place of hopeful monsters in evolutionary biology. *Theory in Biosciences, 3–4*, 349–369.

Tort, P. (Ed.) (1996). *Dictionnaire du darwinime et de l'évolution* (Vol. 2). Paris: Presses Universitaires de France.

Troll, W. (1925). Gestalt und Gesetz. *Flora N.F., 18/19*, 536–565.

Troll, W. (1928). Organisation und Gestalt im Bereich der Blüte. In W. Beneke, A. Seybold, H. Sierp, & W. Troll (Eds.), *Monographien aus dem Gesamtgebiet der wissenschaftlichen Botanik 1*, Berlin: Springer.

Troll, W. (1937). *Vergleichende Morphologie der höheren Pflanzen 1. Teil 1*. Berlin: Bornträger.

Troll, W. (1951). Biomorphologie und Biosystematik als typologische Wissenschaften. *Studium Generale, 4*, 367–389.

Troll, W. (1952). Über die Grundlagen des Naturverständnisses. *Scientia, 46*, 11–18.

Vernadsky, V. I. (1926). *Biosfera*. Leningrad: NHTI.

Vernadsky, V. I. (1965). *The chemical structure of the biosphere of the earth and of its environment*. Moscow: Nauka (in Russian).

Vernadsky, V. I. (1994). *Trudy po geokhimii*. Moscow: Nauka (in Russian).

Vernadsky, V. I. (1997). *Scientific thought as a planetary phenomenon. Nongovernmental Ecological V. I.* Moscow: Vernadsky Foundation.

von Goethe, J. W. (1932). Selected papers. In W. Troll (Ed.), *Goethes morphologische Schriften (Sonderausgabe)*. Jena: Eugen Diederichs.

von Nägeli, C. (1884). *Mechanisch-physiologische Theorie der Abstammungslehre*. Verlag von R. Oldenbourg, München & Leipzig.

Williams, D. M., & Ebach, M. C. (2005). Drowning by numbers: Rereading Nelson's "Nullius in Verba". *The Botanical Review, 71*(4), 355–387.

Wimsatt, W. C., & Schank, J. C. (1988). Two constraints on the evolution of complex adaptations and the means for their avoidance. In M. Nitecki (Ed.), *Progress in evolution* (pp. 213–273). Chicago: The University of Chicago Press.

Zavarzin, G. A. (1997). The rise of the biosphere. *Microbiology, 6*(66), 603–611.

Zavarzin, G. A. (2003). Evolution of the geosphere-biosphere System. *Priroda, 1*, 27–35 (in Russian).