



The history of essentialism vs. Ernst Mayr's "Essentialism Story": A case study of German idealistic morphology

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Abstract

Idealistic morphology as perhaps the most important historical manifestation of typology is very suitable for a historical analysis of Ernst Mayr's "Essentialism Story", which postulates an antagonism between "typological thinking" and "population thinking". We show that German-language idealistic-morphological theories consisted of two clearly distinguishable parts. The cornerstone of these theories was the concept of the type as an abstract pattern representing a certain class of phenomena and embodying the norm of this class. The primary objective of pure typology was to create a non-phylogenetic classification system for living organisms based on structurally explicable characters. Thus, typology, as a non-phylogenetic foundation of idealistic morphology, was conceptually neutral with respect to hypotheses of evolutionary mechanisms. Typology was often accompanied by concepts such as Lamarckism, orthogenesis, creationism, essentialism, etc. These peripheral (with respect to pure typology) concepts were autonomous constructions and did not represent a direct logical consequence of typology. In our view "population thinking", as part of the Darwinian theory of evolutionary mechanism, could not be directly opposed to "typological thinking". Rather, it was peripheral concepts such as essentialism or creationism that led to conflicts between the Modern Synthesis and idealistic morphology.

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Introduction

In one of his last papers (1999) Ernst Mayr (1904–2005) outlined the situation in Germany around the middle of the 20th century regarding the theory of evolution. He pointed out that the developments in the Evolutionary Synthesis can be divided into two periods. The first period was initiated by the publication of *Genetics and the Origin of Species* (1937) by the Russian-born American evolutionist Theodosius Dobzhansky (1880–1959). This period was “essentially completed in 1947, as demonstrated by the Princeton conference and by Rensch’s book” (Mayr, 1999). One can add that by this time (1947) the basic ideas of the Evolutionary Synthesis had proponents not only in the USA (Jepsen et al., 1949) the UK (Huxley, 1942) and Germany (Heberer, 1943; Rensch, 1947), but also in the Soviet Union (Schmalhausen, 1946a, b; Ghiselin, this volume). Thus, the revised version of Darwinism was established simultaneously in three essential language areas: English, German and Russian (Reif et al., 2000).

The second period in the development of the Synthesis, after 1947, Mayr labelled “post-Synthesis” to emphasise that in this period Darwinians were in agreement about the fundamental principles; the post-Synthetic developments just specified and strengthened an already existing paradigm. The post-Synthetic developments proceeded differently in different countries. While English-speaking countries experienced a rapid expansion of the Synthesis, the growth of evolutionary theory in the Soviet Union and, partly, in East Germany was distorted by the political repressions under Lysenkoism (Birstein, 2001; Hoßfeld and Olsson, 2002). Nevertheless, Darwinians continued their research even under these difficult conditions (Hoßfeld, 2001; Levit et al., 2005).

Yet, there was strong scientific opposition to the Synthesis also in democratic West Germany. Mayr reports on the “Phylogenetic Symposium” in Hamburg (1956),¹ 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”. Answering the question “Why then was there so much opposition in Germany?” Mayr (1999) mentions several reasons. The first reason was the typological or idealistic-morphological tradition, which was much stronger in Germany than in English- or Russian-speaking science. The second reason was the “preoccupation of German zoology with phylogeny”, which was again connected with the fact that “the students of phylogeny almost without exception adhered to the idealistic-morphological philosophy”. The third reason was, according to Mayr, a general ignorance about modern genetics among German biologists, which was again related to the adherence of German morphologists and paleontologists to “typological saltationism” (Mayr, 1999). In other words, all the reasons for the resistance to the Evolutionary Synthesis in Germany listed by Mayr are ultimately rooted in one and the same theoretical movement: idealistic morphology, which he equals with typology and essentialism. Accordingly, it was important for Mayr to

¹The “Phylogenetic Symposium” (1956–) was founded as an annual event by Curt Kosswig (1903–1982), Wolf Herre (1909–1997), and Adolf Remane (1898–1976) (Kraus and Hoßfeld, 1998).

show that there is a deep methodological discrepancy between “typological thinking” and “population thinking” and that the only way for the Evolutionary Synthesis to gain a foothold in Germany was to overcome the antagonistic research programme of “essentialism”. He also listed the names of essentialists responsible for the typological sabotage in Germany in both the “synthetic” and the “post-synthetic” period: Edgar Dacqué, Karl Beurlen, Wilhelm Troll, Otto Schindewolf, and Adolf Remane (Mayr, 1999).

Mayr’s formula – “population thinking” vs. “typological thinking” – which reflected this methodological antagonism – can be still ranked as the received view (Winsor, 2003), and even critical writers (e.g., Amundson, 2005) have made little attempt to analyse this opposition taking into account German language typological research programmes, which existed at the time of the Synthesis and thereafter and which, according to Mayr, represented the stronghold of essentialism.

In the present contribution we give an overview of the most characteristic typological theories² in the German-speaking world and show that, although German typologists, in fact, resisted the Darwinian developments in evolutionary theory, it was not the typology itself that confronted the Synthesis, but rather peripheral concepts which accompanied a purely typological methodology. Furthermore, we demonstrate that essentialism, which Mayr equated with typology, is such an auxiliary concept and not an obligatory attribute of typological research programmes.

Ernst Mayr on essentialism and “population vs. typological” modes of thinking

Mayr’s views on typology underwent a significant evolution and were fully formed by 1959 (Chung, 2003). Since that time he interpreted the “population vs. typological thinking” controversy as a key issue in the entire history of both Western philosophy and natural science. He declared that typological thinking is based on an essentialist philosophy (several times he defined essentialism as *ideology* (e.g., Mayr, 1997, p. 428), which can be traced back to Pythagorean geometry. Plato’s philosophy made essentialism more explicit by postulating that “the world consisted of a limited number of classes of entities (eide) and that only the type (essence) of each of these classes of objects had reality, all the seeming variations of these types being immaterial and irrelevant. These Platonian types (or eide) were considered to be constant and timeless, and were sharply delimited against other such types” (Mayr, 2001a). Correspondingly, the basic objective of essentialists was to discover this hidden nature of things. Essentialists dominated the intellectual landscape also in the Middle Ages and well into the modern era. Nearly all philosophers until Darwin’s time, Mayr argues, were essentialists and “all of Darwin’s teachers and friends were, more or less, essentialists” (Mayr, 1991, p. 41).

²Adolf Remane’s views are analysed in detail by Zachos and Hoßfeld in this volume.

Essentialism had direct and harmful consequences for biology, since species were considered to be clearly discontinuous “natural kinds” with constant characteristics (species fixism). It was Darwin, Mayr claimed, who radically improved the situation by perceiving the uniqueness of every individual in sexually reproducing species. This view became a cornerstone of a new mode of thinking – population thinking – and laid the foundation for the natural selection theory. Population thinking proceeded from the assumption that biological reality consists of uniquely different entities, while the statistical mean value is an abstraction (Mayr, 1982, pp. 46–47).

Population thinking was initially brought into genetics by the Russian geneticist Sergej Chetverikov’s (1880–1959) scientific school and further developed by Dobzhansky and Erwin Baur (1875–1933). Darwinian gradualism along with population genetics cleared the way for creating an evolutionary theory based on a revised theory of natural selection. However, even after the establishment of this revised Darwinism a number of scientists refused to accept population thinking because they maintained the archaic mode of typological thinking.

In *One Long Argument* Mayr gave a definition of essentialism/typological thinking as opposed to population thinking: Essentialism is “the belief, going back to Plato, that the changing variety of nature can be sorted into a limited number of classes, each of which can be defined by its essence. Variation is simply the manifestation of imperfect representation of these constant essences. Also referred to as typological thinking” (Mayr, 1991, p. 179).

Given that the typologist thinks in essentialist terms, he is unable to recognise gradual evolution, because there is no gradation between types in his conceptual world: “Since there is no gradation between types, gradual evolution is basically a logical impossibility for the typologist” (Mayr, 1959). Accordingly, typological thinking was made responsible for the hostility of philosophers and even biologists towards Darwin’s original theory and later towards the Synthesis.

Moreover, in the eyes of the “architects” of the Synthesis, typology became responsible not only for the resistance to selectionism, but also for the racist ideology, which played such a tragic role in German socio-political history. Following Dobzhansky (1950), Mayr claimed: “Typological thinking, therefore, is unable to accommodate variation and has given rise to a misleading conception of human races. Caucasians, Africans, Asians, or Inuits are types for a typologist that conspicuously differ from other human ethnic groups and are sharply separated from them. This mode of thinking leads to racism” (Mayr, 1996). Mayr claimed that all racist theories are built upon “typological thinking”: “The typologist stresses that every representative of a race has the typical characteristics of that race and differs from all representatives of all other races by the characteristics ‘typical’ for the given race. All racist theories are built on this foundation” (Mayr, 1997, p. 28).

Typology, as a form of essentialism, thus became the main objective for criticism by the advocates of the Synthesis. Major rivals of the Synthesis such as saltationism and orthogenesis were declared to be the results of typological delusion (Mayr, 1980).

Main concepts in German-language idealistic morphology

All idealistic morphologists subscribed to the same initial idea that the organism is a structural phenomenon and that the purpose of comparative morphological studies must be an exact mental reconstruction of the fundamentals, the typical elements, of this structure. In Germany, the beginning of scientific morphology, and simultaneously of typology, is closely connected with Johann W. von Goethe (1749–1832). Goethe's goal was to explain "the structure of Nature as a whole" (Breibach, 2001), and he looked for a general doctrine of form, for the *idea* of a certain structure, which escapes pure observation and simplistic explanations. This "idea" can be expressed in different forms and can be grasped indirectly by means of empirical studies. Describing plants, Goethe attempted to reconstruct the crucial conformation (*Gestalt*) of nature as a whole hidden behind the observable things. This was the ultimate objective of his idealistic morphology (Goethe, 1790b, pp. 1817–1823). The type was for Goethe an ideal body plan (*Bauplan*) of an organism partly expressed in the basic elements of real organismic organisation: "Thence appears a proposition about an anatomical type, a general entity, which covers (as far as possible) the structures (*Gestalten*) of all animals and allows to specify each animal in a certain system (*Ordnung*)" (Goethe, 1932, p. 315).

Yet, Goethe's structures are dynamic entities. This idea found an expression in his concept of metamorphosis (Breibach, 2001). Metamorphosis is for Goethe a realisation or incarnation of a Proto-plant (*Urpflanze*) in the various actually existing plant structures. It is the metamorphosis that makes the type cognisable for an open-minded onlooker (Goethe, 1790a in Nisbet, 1900). Goethe's concept of metamorphosis makes possible dynamic and functional descriptions of living beings, although it has nothing to do with evolution in a Darwinian sense (Breibach and Ghiselin, 2002). The concept of metamorphic development should not be confused with the idea of organic evolution: just as the Dalai Lama is a reincarnation of Bodhisattva, but not an evolutionary stage, so also all organic creatures are incarnations of the Type, not stages of its evolution. Thus, the first comparative-morphological theories were clearly based on the typological methodology accompanied by teleology and essentialism. Nevertheless, this approach made possible not only morphological, but also physiological studies.

In the second half of the 19th century the theoretical landscape in morphology and evolutionary theory in Germany was dominated by Carl Gegenbaur (1826–1903) and Ernst Haeckel (1834–1919). They succeeded in moving the centre of gravity in morphological research to comparative phylogenetic studies, and Haeckel became known as the leading propagandist of Darwinian ideas in Germany. At the same time, their concepts appear contradictory from a modern viewpoint. Gegenbaur failed to make the methodology of evolutionary morphology consistently evolutionary (historical), and also failed to make it consistently Darwinian. Although the results of his research were presented in phylogenetic terminology, the way he posed the problems was significantly typological (Starck, 1965; Coleman, 1976). Haeckel's Darwinism was accompanied by a strong typological bias as well (Breibach, 2002). Thus, both Gegenbaur and Haeckel, as well as their direct

successors, failed in creating a consistent evolutionary morphology. “Typological thinking” survived in their concepts. As Di Gregorio suggested: “The old wolf had survived in sheep’s clothing” (Di Gregorio, 1995).

In the first part of the 20th century, the theoretical landscape experienced so much influence from typologists – especially in morphology and paleontology – that one can talk about a Renaissance of idealistic morphology in German biological sciences (Meister, 2005a; Levit and Meister, 2005). Almost simultaneously several biologists declared themselves to be adherents of typology. However, unlike the early typology, this new movement, which became known as “idealistic morphology”³ in the narrow sense, saw their typological method as opposed to the method of evolutionary morphology. This movement was represented by E. Dacqué (1878–1945), W. Troll (1897–1978), W. Lubosch (1875–1938), A. Naef (1883–1949), O.H. Schindewolf (1896–1971), A. Remane (1898–1976), and many others. At the same time, idealistic morphology was not at all a methodological monolith opposed to Darwinian evolutionary morphology. The different idealistic morphologists had the basic principles of typology in common, but interpreted the results of typological classification differently. To show the heterogeneity of idealistic morphology and to illustrate the concept of the type and the way it was incorporated into various typological theories, we describe some of these “typological thinkers” below.

Edgar Dacqué

One of the most significant figures in the idealistic-morphological revival was the German palaeontologist Edgar Dacqué (Meister, 2005a). His works were some of the most popular natural-scientific publications of the time (Zimmermann, 1953).

Dacqué was a well-known palaeontologist who had a significant influence on other idealistic morphologists as well as on the general debates concerning evolutionary issues (Rensch, 1980). His book, „*Vergleichende biologische Formenkunde der fossilen und niederen Tiere*“ (Comparative biological form theory of fossils and lower animals, 1921) is regarded as one of the most important contributions to paleomorphology (Reif, 1986). A contemporary of Dacqué, the botanist Werner Zündorf (1911–1943), who was a Darwinian of sorts, labelled his theory as the “supreme manifestation” of idealistic morphology (Zündorf, 1940, p. 16).

Dacqué obtained his doctorate in 1903 from Munich University and was initially an assistant in the Munich Palaeontology Museum. Soon Dacqué established himself as an expert in the field of palaeontology and evolutionary theory and was in 1911 given the extraordinary [ausserordentlicher] Chair for Palaeontology and Stratigraphic Geology at Munich University. However, 1 year later he accepted a position as Curator of the Bavarian Public Paleontological and Historical-Geological Collection, which he held until his retirement. In addition, in 1941, he became director of the Bavarian Paleontological Collection (Meister, 2005a).

³The notion “idealistic” as applied to morphology was probably first employed by Alexander Braun (1862).

Dacqué was active in popularising evolutionary theory (e.g., [Dacqué, 1923](#)). In 1911 he published a paper in a miscellany entitled “Die Abstammungslehre” (The Theory of Descent) with the purpose of making the idea of evolution intelligible to non-specialists. Dacqué participated in this project together with prominent anti-Darwinian theorists such as Richard Goldschmidt (1878–1958), Othenio Abel (1875–1946) and Paul Kammerer (1880–1928). His ideas strongly influenced late advocates of typology such as Adolf Remane (e.g., [Remane, 1956](#)), Oskar Kuhn (1908–1990) ([Kuhn, 1981](#)) and Otto H. Schindewolf.

Dacqué was well known outside Germany, for example, in Russia. Thus, the famous Russian biologist, Leo S. Berg (1876–1950), mentioned Dacqué in his classic anti-Darwinian book “Nomogenesis or evolution determined by law” ([Berg, 1926](#)). A.N. Sewertzoff (1866–1936) – one of the founders of Darwinian evolutionary morphology – refers to Dacqué as one of his theoretical antagonists ([Sewertzoff, 1949](#), pp. 30, 34). Sewertzoff’s pupil, and one of the “architects” of the Synthesis, I.I. Schmalhausen (1884–1963) criticised Dacqué’s idealistic morphology sharply ([Schmalhausen, 1939](#)).

Dacqué left a significant scientific-empirical heritage. His most important contributions to palaeontology include “Grundlagen und Methoden der Paläogeographie” (The Foundations and Methods of Palaeogeography) ([Dacqué, 1915](#)) as well as the voluminous tome *Vergleichende biologische Formenkunde* (Comparative biological morphology) ([Dacqué, 1921](#)) and “Organische Morphologie und Paläontologie” (Organic Morphology and Palaeontology) ([Dacqué, 1935](#)). The latter was welcomed with enthusiasm in professional circles. All in all Dacqué published more than 100 scientific works, half of which were of a theoretical character. He criticised Darwinian selectionism in his early theoretical publications ([Dacqué, 1904](#)) His early work was based on the pure classifying typological approach without the transcendental metaphysics that he would add in later works.. In his *Paläontologie, Systematik und Deszendenzlehre* ([Dacqué, 1911](#)) he still pleaded for the use of “strictly exact methods” and for the avoidance of “speculations”. Under “speculations” Dacqué understood all theories looking for causal explanations of coherencies between organic forms.

Later Dacqué changed his mind and accepted that both competing methodologies are ultimately rooted in metaphysics. In one of his mature and programmatic works ([Dacqué, 1935](#)), Dacqué devoted a voluminous chapter to the methodological questions of morphological research. He claimed that there are two main methodologies in this field. Following Adolf Naef (see below), Dacqué distinguished “systematic” from “dynamic” views of organisms. Both can serve as foundations for morphology. The primary objective of systematic morphology is “to present the whole living world as a stepladder of variously organised forms or types, whose modifications appear as more or less similar or ‘akin’ undertypes and genera, respectively” ([Dacqué, 1935](#), p. 1). The important premise of this procedure and the reason why Dacqué puts the word “akin” in brackets is that a systematising morphologist does not care about the real affinity of the forms he describes. In contrast, “dynamic” morphology concentrates on real descent and on causality. Accordingly, there are two basic morphological methodologies: the

idealistic-morphological methodology and the evolutionary morphology [deszendenztheoretische Morphologie]. The purpose of the pure idealistic morphology is to reduce “various concrete natural organic forms” to *ideal* series of types (Fig. 1). Evolutionary morphology, by contrast, studies the *real* developments and describes “fluctuant” and “accidental” forms (Dacqué, 1935, p. 3).

Yet, both these empirically applicable methodologies, Dacqué argued, have their deep metaphysical roots. The metaphysics that he proposed for idealistic morphology followed Goethe’s morphological philosophy. Dacqué claimed that for idealistic morphology the most important concept is “wholeness” [Ganzheit], which claims that every organic structure is an expression of the so-called proto-form [Urform] immanent in all species. The second basic premise, Dacqué admitted, was the idea that species and genera found in the fossil record can be defined as continuous and morphologically isolated “types”. Transformations [Umwandlungen], mutations and variations of all sorts are only possible within the framework of these “types”. On this basis Dacqué hoped to solve the problem, which occupied him as a palaeontologist and which, in all probability, forced him to take up the idealistic-morphological position, namely, the problem of saltations in the observable fossil record. Based on his typological classifications and the metaphysical principle of wholeness, Dacqué arrived at the conclusion that scientists can only document types as already perfectly adapted species, and that science here enters the sphere of metaphysics. That is why Dacqué’s final definitions of type are vague and quite speculative: “Types – so far as we can talk about them in an intelligible way – are potential species [Artpotenzen] realised in actual forms and

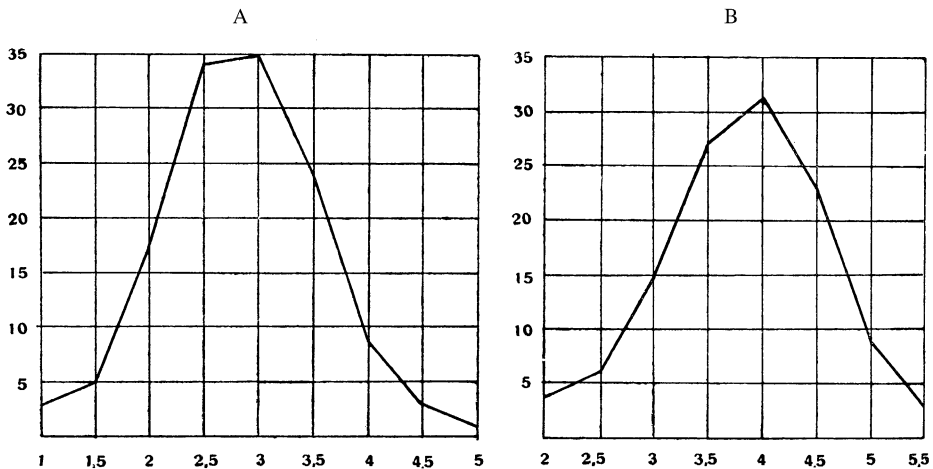


Fig. 1. Dacqué’s way of establishing formal (initial) types by a purely morphological-statistical procedure: The variation curves for the proportion of length and width of (A) *Rynchonella lacunosa* from the upper Jurassic of Moravia; (B) of *Cidaris monilifera* from the upper Jurassic of Württemberg. The formal type is a morphological average: “The type is the culmination, which is represented by most of the individuals.” (Dacqué, 1921, S. 188). All Dacqué’s essentialistic metaphysics was based on such empirical studies.

underlying these forms. They are not simply abstractions from the concrete forms, but are ultimate genotypic realities and potentials [Potenzen] beyond the objective-phenotypic realities” (Dacqué, 1921, pp. 728–729).

So Dacqué advocated a metaphysical-creationist approach to the problem of gaps in the fossil record. According to him, every paleontological epoch preserves a certain “Zeitgeist”, which finds its expression in “types” existing beyond the material world, but at certain moments taking an active part in the evolutionary drama. The transformation of a type is, however, a directed process. This “entelechy” is essential for an understanding of what he calls “type”: Type is a potentiality partly realising itself in the actually existing species. Accordingly, the fossil record does not reflect evolution as it is, but rather gives only an indication of what goes on behind the visible world. That is why in his later works Dacqué calls his theory of descent a “theory of development” (Entwicklungslehre) instead of a theory of evolution (Deszendenzlehre). Development is directional and the end result is humankind. So for Dacqué human beings are the pinnacle, but not the end, of evolution. The true purpose of his mature theory is to show that the entire evolution (= development) is a teleological process aimed to produce and to perfect humankind: “The entelechy ‘man’ is a continuous ‘prototype’ [durchgehende ‘Urform’] existing from the very beginning” (Dacqué, 1932/33, p. 90). He argued that the very idea that “higher” forms can develop from “lower” ones contradicts sound logic.⁴ Only the reverse procedure is reasonable, because nothing can appear out of nothing. Only already pre-existing forms can later come into being. Evolution appears to be an unfolding of a divine plan, which realises itself in sudden saltations followed by long periods of phylogenetic stability. This leads to an important statement, that man has no ancestors. Man is the ultimate cause and the final goal of evolution, which has not changed its course since the stage of single-celled organisms.

Wilhelm Troll

The idealistic morphology of the botanist Wilhelm Troll (1897–1978) is both less metaphysical and less explicit than the theory expounded by Edgar Dacqué (Meister, 2005b). Troll, like Dacqué, studied at Munich University, where he defended (1921) a doctoral thesis titled “On the Stamen and the Movements of the Style from the Teleological Viewpoint”. After his “Habilitation” (1925) Troll taught as a “Privatdozent” at the Botanical Institute of Munich University. Six years later Troll became an extraordinary [ausserordentlicher] professor and in 1932 he obtained a full professorship for botany at the University of Halle (Saale). After deportation by the American authorities after WWII, he became director of the Botanical Institute and Botanical Garden in Mainz (1946–1966).

Even at the beginning of his scientific career Troll was strongly influenced by Goethe’s typological morphology. As early as 1922 he published a paper devoted to Goethe’s scientific worldview. A few years later Troll wrote his programmatic paper “*Gestalt und Gesetz*” (Structure and Law), where he explicitly credited his

⁴And this is why any kind of racism is unthinkable in his conceptual world.

understanding of morphology to Goethe and contrasted Goethe's views sharply with those of Immanuel Kant (1724–1804). In this unusually concise and clear paper Troll summarised his general methodological platform based on Goethe's ideas.

Troll outlined a dialogue between Goethe and Friedrich Schiller (1759–1805), which took place as they were on their way back to Weimar from a meeting of the natural science society (Naturforschende Gesellschaft) in Jena (Troll, 1925). Goethe argued that one should explore Nature “as it is”, i.e., as an acting and vivid whole without breaking it up into separate pieces. He illustrated this idea by his concept of a “primordial plant” [Ur-Pflanze]. Schiller was unhappy with Goethe's illustration and complained that Goethe only attributed his own ideas to Nature. Schiller's objection is crucial for Troll and the entire paper is an attempt to substantiate the contrary position. Troll started from the assumption that there are two modes of cognition: (1) A “discursive-analytical ability” as articulated by Kant and (2) an intuitive ability or “judgement through intuitive perception” [anschauende Urteilskraft] as represented by Goethe (Troll, 1925, pp. 540–541; Goethe, 1932, pp. 289–290).⁵ In other words, Troll distinguished rational-logical and intuitive modes of cognition. The discursive-analytical ability is useful in sciences such as physics, but fails in morphology because “an organism has a certain independence in relation to the causal events and controls them more than it itself is controlled”.⁶

Understanding 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”. It is this intuitive way of cognition, “a spiritual eye”, which makes possible an insight into the very essence underlying the observable level of being. Troll writes that this intuitive, imaginative mode of cognition is truly essential for Goethe's morphology, while the Kantian analytical way is used 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.

It might appear astonishing that this intricate research programme had considerable empirical success. Troll's main work entitled *Vergleichende Morphologie der höheren Pflanzen* (Comparative morphology of the higher plants), which appeared in several volumes (Troll, 1937, 1939, 1943, 1971) and laid the foundation for German-language morphological botany, together with several papers dealing with technical problems (Troll, 1964, 1969) was given substantial international recognition (Weberling, 1981). After WWII, Troll became an influential figure in German plant morphology (Nickel, 1996; Claßen-Bockhoff, 2001) and was arguably the leading German idealistic morphologist (Junker, 2004, p. 344).

⁵The German term “Anschauende Urteilskraft” is difficult to translate, and different translations exist in the literature. “Judgement through intuitive perception” was used by Walter Heitler and his translator Frederick Amrine in Heitler, W., 1998. *Goethean Science*, in: Seamon, D., Zajonc, A. *Goethe's way of science – A Phenomenology of Nature*. State University of New York Press, New York. pp. 55–69.

⁶German original: “Ein Organismus behauptet dem kausalen Geschehen gegenüber eine gewisse Selbständigkeit und ‘benutzt’ es mehr als er in ihm aufgeht”.

Troll's emphasis on empirical research can be explained by the specificity of his methodology. He started with descriptive-comparative studies, i.e., by measuring and comparing various plant characters in order to find common traits in the diversity of forms (Fig. 2). This allowed Troll to construct the “circles of types” [Typenkreise], which defined the limits of and modifications of certain types (Troll, 1951, p. 380). The types reconstructed in this way are based on analogies rather than the homologies important for studies of phylogeny (Troll, 1928, VII). Through the study of analogies comparative morphology is able to show that plant structures (Troll emphasised that it is especially evident in botany) cannot be reduced to their adaptive values and that they obey immanent structural regularities. Troll maintained that Darwinians, with their concentration on adaptations to the environment, are in principle unable to deal with this issue.

So the modifications of the type in Troll's morphology reflect the structural interrelations and never a real series of forms going from ancestor to descendant (Troll, 1928, p. 20). The discovered structural laws are not simple generalisations or abstractions but reveal objectively, “in reality” existing regularities. These regularities can be applied, for example, to predict the existence of hitherto unknown forms. The “ideas” of idealistic morphology, Troll argued, are not just creations of the imagination, and Troll labels them *platonian* in that sense.

These ideas can be perceived by means of morphological intuition. According to Troll, there are three essential instruments in an empirical science: description [beschreiben], explanation [erklären] and representation [darstellen]. Proper morphology, Goethe's morphology, is based on representation: “The morphology founded by him is a great distance away from the causality principle and is completely based on representation [Darstellung]” (Troll, 1925, p. 556). The purpose of “representation” is to comprehend an organism as a whole. The proper method for fulfilling this purpose is *comparison*. In short, this is how Troll justified his views on comparative morphology. He never abandoned these methodological foundations and also his later morphological works are characterised by this belief.

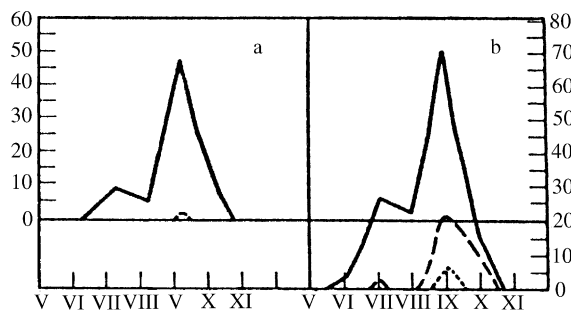


Fig. 2. The graphical representation of variation by the ramification of *Viola* inflorescences: left picture (a) – without fertilisation; right picture (b) – fertilised. The variation of the inflorescences was documented during 1 year (roman numerals = months) (Troll, 1941, p. 137).

Yet, the final purpose of Troll's intuitivism goes far beyond morphology. He postulated the existence of an immanent creative principle which creates perfectly adapted organismic plans [Organismenpläne]. The peculiarity of living beings is determined by "thoughts and ideas of a creative power which penetrates from the ideal world [Welthintergrunde] into nature, which gives new characteristics to matter and creates the type-like basic organic forms"⁷ (Troll, 1937, VI). In one of his last published papers he made his views even more explicit: "God displays himself in the same manner in the phenomena of the natural world, which in this way become a reflexion of his completely different essence"⁸ (Troll, 1952, p. 13).

That is why the "type" as delineated in Troll's metaphysics is a way to obtain an essential and even divine truth about living beings. Without doubt Troll's theoretical system, as well as Dacqué's, was based on essentialist philosophy.

Adolf Naef

Adolf Naef was one of the crucial figures in idealistic morphology but, at the same time, he attempted to stay within the framework of the established empirical sciences and the pure typological method, without straying into metaphysical and religious-like generalisations in the manner of Troll or Dacqué (Meister, 2005c).

Naef studied to become a school teacher at the philosophical faculty of Zürich University (Switzerland). In 1909, he obtained his Ph.D. in Jena (Germany) and 1 year later Naef moved to the "Stazione Zoologica" in Naples (Italy). Until the beginning of WWI Naef worked at the paleontological museum in Munich, but later (1915) he was given a "Privatdozent" position in Zürich, where he defended his *Habilitationsschrift* in 1917. However, because of the difficulties in finding a position in the German-speaking countries he moved to the University of Zagreb where he accepted an extraordinary professorship (1922–1927) at the medical faculty. In the mid-1920s he visited Stazione Zoologica di Napoli again, where he had long discussions with A.N. Sewertzoff, the founder of Russian evolutionary morphology (Levit et al., 2004). Sewertzoff influenced Naef's views on the interconnectedness of ontogeny and phylogeny. Naef became a full professor at the Egyptian University in Cairo (1927), a position he held for 12 years and lost as a consequence of WWII (Reif, 1998; Meister, 2005b).

Naef's primary scientific focus was on molluscs (Naef, 1911a, 1911b, 1913). His early work dealt with the biology of cephalopods (Naef, 1923a). He saw it as his task to create a new "synthesis", i.e., to revise the foundations of morphology within the context of a broad theoretical perspective. His new morphology was to be built on the "sound foundation of old idealistic morphology" (Naef, 1919, p. 13).

⁷German original: "[...] Gedanken und Ideen einer aus dem Welthintergrunde in die Natur hereinwirkenden schöpferischen Macht auf, welche, der Materie neuartige Ausprägungen verleihend, die typenhaften Grundformen organischer Gestaltung ins Dasein rief".

⁸German original: "Gott entäussert sich gleichsam in die natürlich-welthaften Gegebenheiten hinein, die so zu einem geschöpflichen Abbild seiner ganz andersartigen Wesenheit werden".

Naef, as well as Dacqué and Troll, found this “sound foundation” in the works of Goethe (Breidbach, 2003). His basic assumption was that the world of living beings can be described in terms of a hierarchical classification system organised according to the increase in degree of generality. He proposed that within this natural system one can distinguish more or less clearly definable units, which can be thought of provisionally as types: “The knowledge of the typical within a certain more or less restricted group [...] can be gained through factually and logically based abstraction” (Naef, 1923b, p. 391). The method to use is comparative morphology, by which it is possible to separate general features from particular ones. In this way Naef abstracted, from the diversity of random variations, a network of correlated general characters, which compose a type (Naef, 1923b, p. 390). The type, according to Naef, is a kind of mathematical abstraction, but it can also be (actually or potentially) incorporated into a specific organism (Fig. 3). All variations around a certain type shape, the “circle of forms” [Formenkreis] and can be deduced logically. Naef’s method is to first draw together knowledge about the type inductively, and



Fig. 3. The general type of Metatheria (marsupials) (Naef, 1931, p. 98). The picture illustrates that for Naef the type is an abstracted average of all marsupials, reflecting their most characteristic features. At the same time the type is a realisable entity.

then to deduce all possible forms. The sum total of the “circles of forms” builds the foundation for a new systematics.

Naef labelled his approach *new synthesis* or *systematic morphology*: “Systematic morphology is, thus, a rational synthesis of ‘comparative anatomy’, ‘palaeomorphology’, ‘embryology’, and ‘natural systematics’ and is, in agreement with its purpose, juxtaposed to the dynamic morphology aimed at analysing the processes of the occurrences of form in accordance with the laws of physics and chemistry” (Naef, 1917, p. 15). Systematic morphology should have put the “forms” in a good order by describing the locations of different forms in the system as a whole. It is a descriptive science and Naef attached much importance to the descriptive nature of his systematic morphology. Its importance for evolutionary theory follows from its descriptive nature, because description is needed for discovering the innate logic of the origin of forms.

For Naef the type was a common proto-form [Urform], which could be discovered by comparison of a range of organic structures. This descriptive procedure was primary in relation to any evolutionary explanation or theory, which had to be built on the basis of empirical studies and not vice versa. The forms in question are “similar” if they can be deduced from an imaginary or real proto-form in the simplest possible way, i.e., through the shortest morphogeneses. It is this form, derived from a comparison of many different structures, which is labelled a type. The type can simultaneously be both an abstraction and – sometimes – an existing structure: “Thus the type is for us a purely imaginary form, the idea of a natural being [Naturwesen]”, but at the same time the type is an “absolutely possible” form (Naef, 1919, p. 13). It is an abstract form, which can be filled with a precise morphological content: “The type of snails is a conceivable [gedachte] snail, the type of vertebrates is a conceivable vertebrate” (Naef, 1917, p. 17). Naef compared biological objects with crystals fluctuating around certain reproducible mathematical abstractions, while rarely completely corresponding to these abstractions.

The “old” synthesis was, according to Naef, created by Ernst Haeckel: “The efficiency of the post-Darwinian period consisted, first of all, in discovering numerous facts and series of facts [Tatsachenreihen] of an anatomical evolutionary nature, which, mostly unconsciously, resulted in examining and completing *Haeckel’s brilliant synthetic construction* [our italics]” (Naef, 1917, p. 4). Because Naef saw the quintessence of Haeckel’s research programme in the “biogenetic law”, he subjected Haeckel’s concept to significant revision. In fact, Naef proposed a modernised form of the “biogenetic law” within the framework of his own morphological theory.

Naef’s type is less a platonic “idea” than Troll’s and Dacqué’s type, but rather a scientific model free from mystical features. Naef’s morphology was a *dynamic* theory of phylogenetic–ontogenetic relations. This dynamism is clearly expressed in his concept of cycle which is essential for his theory: “The development of life is in its most general form a cyclical process” and this cyclicity “is the fundamental fact in the establishment of organic forms” (Naef, 1917, p. 24). The proto-form of the whole development is the cyclic-rhythmical development (e.g., bacteria, cells), although morphological reality is much more complex than just a pure cyclicity. The

multicellular organisms develop by means of terminal processes (terminality means here death or degeneration of the *soma*), which Naef termed *morphogeneses*. Yet, morphogeneses are not truly terminal, because they are based on germinal development, which is, again, of a rhythmic-cyclic nature. This dynamic approach allowed Naef to reformulate Haeckel’s “biogenetic law” as the “*law of terminal modification*”: “Stages of morphogenesis are as conservative in the recapitulation of initial development, as they are close to its beginning, while the more progressive, the closer it [the morphogenesis – *auth.*] is to the end” (Naef, 1917, p. 57) (Fig. 4).

So Naef’s *law of terminal modification* is not a negation, but rather a refinement of Haeckel’s biogenetic law. This law has a central position in Naef’s theoretical system and explains how idealistic morphology is at all possible. The concepts of ‘type’, ‘typical similarity’ (or dissimilarity), together with the ‘law of terminal modification’ are essential instruments for creating a ‘natural systematics’, i.e., for ordering living beings in accordance with their phylogenetic affinities. Naef’s method of creating imaginary types should have been especially effective for reconstructing large gaps in the fossil record. It is important to emphasise that transitional forms between various types are real “forms” according to Naef. If we accept Mayr’s definition of essentialism as a belief in “sharply delimited types” (Mayr, 2001b, p. 286), it is evident that Naef’s typology was not a kind of essentialism. In sharp contrast to Dacqué’s creationism and Troll’s neo-platonism, there is no need for supplemental essentialist explanations in Naef’s reconstructions of phylogenetic history.

Accordingly, it was important for Naef to keep a balance between his theoretical assumptions and empirical inquiries. This can be seen, first of all, in his scrupulous work on specific issues of the morphology and phylogeny of molluscs, especially cephalopods. One of his most significant early books is “*Studien zur generellen Morphologie der Mollusken*” (1911, 1913, 1924, Studies of the general morphology of molluscs) and “*Die Cephalopoden*” (1923a). In later periods Naef worked on vertebrates, especially tetrapods (Naef, 1931) and made significant inquiries into

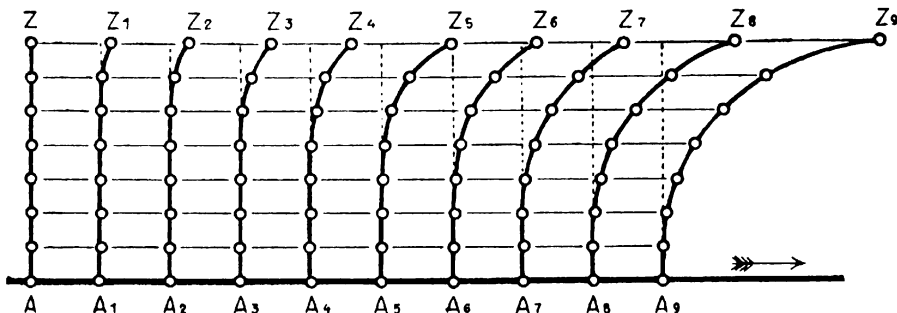


Fig. 4. Haeckel’s biogenetic law in Naef’s interpretation (left) and Naef’s own “law of terminal modification” (right). The vertical lines symbolise ontogenetic pathways. Horizontal heavy lines manifest the continuity of the development from one egg cell to another. From the typological viewpoint, the “terminal modifications” mean the gradual transition of one type into another (from Naef, 1917, p. 11, 57).

embryology, an activity which was stimulated by the necessity to prove his law of terminal modifications.

Otto Heinrich Schindewolf

Schindewolf was the most influential paleontologist in post-war Germany and his theory of evolutionary change dominated German paleontology (Reif, 1993; Meister, 2006). Schindewolf studied at the Universities of Göttingen and Marburg, where he got his doctoral degree under the supervision of Rudolf Wedekind (1883–1961), a paleontologist who applied statistical methods to analysing the fossil record. Schindewolf taught in Marburg until he moved (1927) to Berlin to the Department of Paleozoology at the Prussian Geological Institute (Preussische Geologische Landesanstalt). In 1933, he became director of the Institute. After the second World War Schindewolf for a short time acted as paleontology Professor at the Humboldt University in Berlin (1947), but a year later he was given a Chair in Geology and Paleontology at Tübingen University, which he held until 1964. Schindewolf died in 1971, and was active until his last years.

Schindewolf championed a complex theory embracing saltationism, orthogenesis and typology. He advocated typological methods even in his later work. In a paper from 1962 he complained about the decreasing influence of typology/idealistic morphology, which was unjustly categorised as a subjective approach to morphology. Yet, in Schindewolf's opinion it was the Darwinians who had pushed morphology towards the unsteady ground of transient hypotheses: "The old morphology⁹ 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. There can be no systematics under the dictate of phylogeny. On the contrary, phylogeny and evolutionary theories are logically secondary to systematics, which is autonomous: "The primary mission of systematics is to classify morphological facts, not [to produce] phylogenetic hypotheses" (Schindewolf, 1962, p. 59).

Schindewolf's high regard for typology and his dissatisfaction with the "new systematics" and Mayr's definition of species had nothing to do with "essentialism". Schindewolf's concern was the applicability of this definition in the praxis of paleontology. Thus, analysing Mayr's famous species definition ("Species are groups of actually (or potentially) interbreeding natural populations which are reproductively isolated from other such groups", Mayr et al., 1953, p. 25) Schindewolf claimed that it is hardly applicable to fossil species: "This definition might be theoretically incontestable, although a serious shortage is that such a 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" (Schindewolf, 1962, p. 65). To avoid these difficulties Schindewolf proposed a definition of species that could be applied to classifying fossil remains:

⁹Old in the sense of pre-Darwinian.

“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” (Schindewolf, 1962, p. 67). With this definition he proclaimed the priority of morphological methods in paleontology, but there is nothing specifically essentialist in the proposed criteria.

Based on this historical and logical priority of morphology Schindewolf created his theory of “typostrophy”. 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 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. Schindewolf called this process proterogenesis (Schindewolf, 1936, p. 26, 101) and 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 (Schindewolf, 1952). 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. This position led him to an interpretation of evolution, within which the question of the origin of types was never seriously asked, and Schindewolf was unable to explain the mechanism of appearance of new “body plans”. 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 favoured 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 characterised by slow progressive development of a new type driven by natural selection, which is degraded to a subsidiary evolutionary mechanism (Rensch, 1980) responsible for the occurrence of minor adaptations in the “body plans and operating within the framework of 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-specialised 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. His arguments against the Darwinians were also based directly on comparing their claims, e.g., that evolution is gradual, with what he observed as a paleontologist. It is extremely difficult to find essentialist statements in his papers. His typology was based on the practical needs of identification and classification of the fossil remains and free of explicit metaphysics.

Methodological concerns: what is wrong with the “Essentialism Story”?

In his recent book Ron Amundson (2005) criticised Ernst Mayr's “Essentialism Story” and the connection Mayr makes to species fixism as an anti-evolutionary mode of thinking: “Essentialism is a doctrine about natural kinds, not about the causal relations between these kinds. Its paradigmatic application is to items like geometric figures: A triangle cannot change into a square because their essences are distinct. In contrast, species fixism is a doctrine about causal relations – the causal relation of *generation* between parents and offspring. Essentialism may entail that a dog cannot transform into a cat, but it cannot (by itself) entail that a dog cannot *give birth to a cat*” (Amundson, 2005, p. 209).

This is definitely to the point if applied to the essentialist elements in the idealistic-morphological theories described above. The question is, however, whether it is generally correct to think, as Mayr did, that typology equals essentialism. In other words, we assume that the first step in the formula “typology = essentialism = species fixism” is at least as problematic as the second. Below we reformulate Mayr's “Essentialism Story” by subdividing it into three major theses and test its applicability to 20th century typology.

The first thesis of the “Essentialism Story” is that as a form of essentialism, “typological thinking” must have been opposed to the Darwinian explanation of evolution in terms of “population thinking”. In this view, typology is opposed to rational, causal explanations of the phylogenetic history. The primary objective of any mature typology was to reconstruct and compare the body plans of the biological objects in question (for example, paleontological findings), in order to classify them. The question about the causal relationships between these objects does not appear in the framework of pure typological analysis, and there is even no way of posing this question by means of typological theoretical tools. Even the most radical advocates of typology realised that typological reconstructions do not reflect the causally determined phylogenetic history. Thus, Dacqué wrote: “Not until we establish the typical [forms] in that we separate the incidental [forms] from the fundamentally typical [forms] by means of biological research, can we make conclusions about the internal affinity of these forms. However, doing this we leave the real phylogenetic history and move to idealistic morphology” (Dacqué, 1921, p. 727). Troll expressed this idea with all possible clarity: “Morphology in its purest characteristic knows no question of cause. The concept of causality is – as a minimum – alien to morphology as well as the conceptual-analytical procedure”

(Troll, 1925). Typology was understood as a tool for doing systematics and was not instrumental for discussing evolutionary mechanisms of any kind. As Schindewolf put it: “Systematics¹⁰ as such – in accord with its essence – possesses a logical autonomy and this independence must be asserted unconditionally. Its categories are the circles of types and body plans. In the face of the hypothetical and fluctuant character of phylogeny, phylogenetic views and concepts should be kept out of systematics to prevent decay of this conceptually perfectly founded and – as a consequence of its purely descriptive nature – inviolable system” (Schindewolf, 1927).

Similar views were shared, implicitly or explicitly, by the majority of idealistic morphologists. They all saw typology as an instrument of pure, “typological” systematics. Therefore, the idealistic morphologists made a clear distinction between their “ideal” systems and the “real” phylogeny. Wolfgang Hagemann, one of Troll’s students, recalled: “We have set ourselves as a target to clarify the way in which comparative morphology must operate.[...] We had no doubts that the works of Troll (1937–44, 1964–69) gave the best foundations for this, even though the question of phylogenetic relationships was of no interest to him” (Hagemann, 1975, p. 107).

Thus, pure typology was not essential for rejecting or accepting causal theories of descent, because it is a research programme operating in another theoretical dimension. Typology contents itself with classifying organismic structures around certain abstract models, which it calls “types”. It can, however, be “complementary to causal approaches” (Gleißner, 2005). There are no obstacles to incorporating results of typological research into other theoretical contexts: metaphysical, theological or evolutionary. Moreover, there are no logical obstacles to adapting the typological way of classification to the Darwinian research programme. Recently, Richardson et al. (1999) came to the conclusion that “typological thinking” can be applied to the study of embryonic development. In accordance with the principles of typology, they assume that “archetypes are not real entities, but idealised constructions based on artificial selections of characters” (Richardson et al., 1999). Although typology can only be applied to the analysis of evolution and development to a limited degree, there is no great danger in doing so for the evolutionary paradigm: “Within the evolutionary paradigm, we believe, that archetypes represent no more than selected clusters of conserved features associated with a particular taxon” (Richardson et al., 1999). In short, typology is not opposed to causal explanations of evolution, but can be incorporated into various explanatory systems.

The second thesis is that typological theories, as a kind of essentialism, propagated the idea of the type as an invariable entity, which is “sharply demarcated against all other such essences” (Mayr, 2001b, p. 74). This is, in Mayr’s eyes, the direct way to species fixism. In fact, there is no logical necessity for the rigidity and non-transformability of the type in the pure typology and, if needed, one can also construct a dynamic model of the type (Troll, 1928, p. 35). Also, the typological

¹⁰Schindewolf means typological systematics.

method does not necessarily require that types are sharply demarcated. In typology, types are mathematical abstractions and it depends on the level and methods of abstraction and on the purposes of the researcher, whether the derived types have sharp boundaries or gradually flow into each other. In other words, “there are as many types and findings as they are scientific perspectives” (Claßen-Bockhoff, 2005). In the history of idealistic morphology the question of the boundaries of the type has been answered in accordance with the needs of the theoretical system into which the typological method was integrated.

The idealistic-morphological theories never consisted of typology only. In the majority of cases, typology was just one part of a theoretical construction incorporating various theoretical elements such as neo-Platonism, Christian theology, mutationism, orthogenesis and so on. The question of constancy or transformability of the type was connected with the question of the constancy or evolution of taxa, which was posed not in typology itself but in the auxiliary concepts, which accompanied every historical form of typology. The answer to this question was dependent on these auxiliary concepts. Thus, Naef’s reconstructions of phylogenetic history implied the idea of species evolution. He not only allowed transitional forms between various types, but also suggested a mechanism (the law of terminal modifications) to explain gradual variation from both phylogenetic and ontogenetic perspectives. In contrast, in Dacqué’s theory any transitions between types are forbidden. This is because in his theoretical system, the origin of types was given a creationist explanation in the framework of a Christian theology.

Schindewolf on the other hand, did not see any transitional forms between classes and orders, but not for typological reasons. His morphological and paleontological studies convinced him that types are perfectly and coherently established forms, and that the fossil record shows no transitions between these forms. So Schindewolf proposed that the only possible mechanism for explaining these *empirical* facts is macromutations. Here he repeated Walter Garstang’s words about the first bird hatching from a reptile egg. Yet, there is nothing mystical or specifically typological about this metaphor. Schindewolf simply stated that the only mechanism he can propose for the first phase of evolutionary development (typogenesis) is sudden saltations, which happen in early stages of ontogenesis, although, he argued, there are no reliable theories which explain their exact mechanism. Some idealistic morphologists were not explicit in the question of the origin of types and the possibility of transitional forms. Troll, for example, mostly avoided both putting and answering this question, but the logic of his typology does not prohibit transitional forms.

Thus, using Amundson’s “cats and dogs” metaphor, one can say that in the history of idealistic morphology, a variety of procedures were allowed: cats could give birth to dogs by means of macromutations (Schindewolf); cats could gradually transform into dogs due to “terminal modifications” in ontogeny (Naef); cats never transform into dogs because of their essentially different nature (Dacqué). This diversity of interpretations illustrates our claim that pure typology does not imply any restrictions on evolutionary interpretations. As Schindewolf phrased it: “The crucial point of idealistic morphology, i.e., non-phylogenetic morphology, consists in

comparing organic forms, in inquiring into their gradual similarities as well as in establishing their coherences” (Schindewolf, 1950, p. 471).

The third thesis in Mayr’s essentialism story claims that typologists were unaware of individual variation, while “populationists” made them into the cornerstone of evolutionary theory. Arguing in favour of “population thinking” Mayr postulated: “Individuals, or any kind of organic entities, form populations of which we can determine only arithmetic mean and the statistics of variation. Averages are merely statistical abstraction; only the individuals of which the populations are composed have reality” (Mayr, 1997, p. 28). By irony of fate, this thesis reflects the position of the majority of adherents to idealistic-morphological theories. For instance, Troll was very aware of individual variations, which were thoroughly documented in his empirical studies, because the easiest way to construct an initial type in scientific praxis was to describe individual variations and then to find an average, using statistics. Methodologically different reconstructions leading to the establishment of a new type were based on this statistical initial procedure in the majority of theories (Figs. 1, 2, 5). It is, however, important to distinguish between paleontologists (Dacqué, Schindewolf) and neontologists (Naef, Troll). The latter could take individual variation into account much better than those working with limited fossil material. In contrast to neontologists, paleontologists were forced to operate with a much less abundant material of variation; therefore, their types are of a higher level of abstraction, although this does not mean that the abstracted characters have no correspondence to reality. Schindewolf has a direct response to Mayr’s accusation that he abandoned variation in favour of the “type”. After quoting Mayr’s passage on typological thinking as “a concept in which variation is disregarded and the

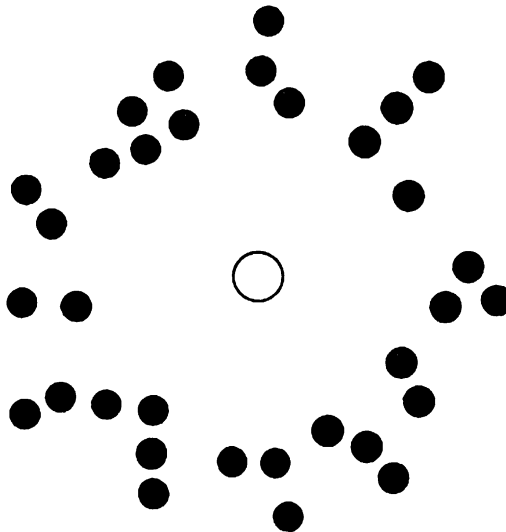


Fig. 5. Troll (1928, p. 34) on the type as an abstracted average of variations delimited by the so-called “circle of forms” (“Der Typus inmitten eines Formkreises”).

members of a population are considered as replicas of the type, the platonic *eidos*” (Mayr, 1963, p. 673), Schindewolf writes: “This definition can only be based on a misunderstanding; it is, in my view, factually wrong and does not correspond to the concepts of modern ‘typologists’, which I would simply call morphologists” (Schindewolf, 1969, p. 12). “Nobody doubts nowadays”, Schindewolf continued, “that populations are the stronghold of evolutionary change [der Hort der Entwicklung]” (Schindewolf, 1969, p. 14), however, the type is not less real than the population: “It [the type] is certainly not just a phantasm [Hirngespinnst], a platonic idea, a nominalistic notion, but a natural-scientific reality, which must be accepted as well as the reality of populations” (Schindewolf, 1969, p. 15).¹¹

Schindewolf in the above quotations spoke not only for himself but also for the typologists as a theoretical movement. This implies that the post-war typologists were aware of population biology and took the arguments of Darwinians very seriously. But despite realising the importance of individual variation and understanding “population thinking”, the typologists emphasised generalisation in their work. The primary objective of typology was classification. No classification system concentrates on the unique features by avoiding generalisations. Any classification implies *per definitionem* the search for common features, and typology looked for the essential structural characters. There is no immanent anti-evolutionism or essentialism in this procedure.¹²

An important sideline of Mayr’s thesis on the failure of typologists to appreciate the importance of individual variation, was his assertion that typology leads to racism. However, this argument is flawed from both a logical and a historical perspective. From the logical perspective, pure typology is the worst instrument for creating a biological theory to discriminate between human races. Typology is a method of creating abstract types and systems for classifying these types. It does not imply a “higher–lower” scale, as many typologists explicitly stressed (e.g., Dacqué, 1927, p. 55) and consequently it is not possible to argue that “Caucasians” are better than “Africans” in the framework of “typological thinking”. Even if it would be possible to demonstrate that there are different types within the major type “mankind”, this typologisation would not necessarily include the concept of hierarchy.

A “higher–lower” value scale could appear in a typologically based theory due to an auxiliary concept. However, we know from history that none of the German typologists mentioned above supported racism during, before or after the Third Reich. On the contrary, Darwinism with its phylogenetic trees, “earlier–later” and “higher–lower” differences and “struggle for existence” was much easier to use for

¹¹One can see a contradiction in Schindewolf’s declaring the “ideal” character of typology and at the same time claiming that the types are not less “real” as populations. Yet, Mayr’s populations are described in statistical terms and only individuals have reality (Mayr, 1997, p. 28). So Schindewolf’s “not less real” means that types are as real as populations, i.e., that the typological kind of abstraction is not less empirically based than that of the Synthesis. Types in idealistic morphology are “real” or “descriptive” as far as they are reducible to empirically testable characters.

¹²One could argue that there is some essentialism in Schindewolf’s search for “essential” characters (e.g., Reif, 1997); however, it would not be “essentialism” under Mayr’s definition.

the racist ideology then typological interpretations. This can be proven easily in the historical records. Unlike the idealistic morphologists, the majority of Darwinians were passively or actively involved in national-socialist organisations (Junker and Hoßfeld, 2002).

To summarise, typology, as applied to 20th century biology, was a method of classifying organismic groups by establishing generalised and abstracted features. An initial and very specific step of typology was to look for (typical) common traits in the biological diversity, and to create ideal models of these groups of organisms. No direct references were made to causally determined processes on this purely typological level. Typology is not the same as “essentialism” and “idealistic Morphology”, as Mayr argued. Idealistic morphology is a historical phenomenon, a theoretical movement, which in its supreme manifestation can be found in 20th century Germany. The idealistic morphologists used the typological method as the foundation for their research programmes. However, typology was only one element (although important) of their theoretical systems, which also included further elements like creationism, phylogeny, mutationism, orthogenesis, neo-Lamarckism and so on. These auxiliary explanatory elements can entail a kind of essentialism, but it is not evident in the case of typology itself.

Consequently, typology has little to say both about a fixed number of species and generally about the nature of the features it describes. The “type” in typology is a pure mathematical abstraction, which can be incorporated into essentialist metaphysics and into Darwinian or Lamarckian theoretical models with equal success.

Résumé

In the idealistic-morphological theories described in this paper, two major constituting parts can be distinguished. The cornerstone of these theories was the concept of the type as an abstract pattern¹³ representing a certain class of phenomena and embodying the norm of this class. The primary objective of pure typology was to create classification systems for living organisms based on structurally explicable characters without references to phylogenetic history or causal explanations. Typology, as a non-phylogenetic foundation of idealistic morphology, was conceptually neutral with respect to evolutionary mechanisms.¹⁴ “Population thinking”, being a part of the Darwinian theory of evolutionary mechanism, could therefore not be directly opposed to “typological thinking”.

¹³Some authors, for example, Naef, view the type as an abstract pattern, but this does not exclude the existence of its analogue in reality. Likewise, symmetry in geometry is a mathematical abstraction, but this does not exclude the existence of almost ideal symmetrical crystalline structures.

¹⁴Reif (1997) came to a similar conclusion about Schindewolf’s typology: “Schindewolf showed that there was neither coincidence (nor an inner contradiction) but a logical link between his typology, his phylogenetic methods and his theory of mechanisms of evolution”.

Yet, only a few idealistic morphologists propagated a pure typology. Idealistic-morphological theories consisted of typological methodology accompanied by other elements, such as Lamarckism, saltationism, creationism, mutationism, orthogenesis and natural selection mixed into a unique theoretical structure. These peripheral (with respect to pure typology) concepts are autonomous constructions and none of them is a direct and inevitable logical consequence of typology. Peripheral concepts were, however, responsible for answering questions about the nature of types and their relation to real organisms, although not in all theoretical systems were these questions formulated explicitly. In idealistic-morphological theories one can find the whole spectrum of answers to these questions. Interpretations range from Naef's evolutionary gradualism to Dacqué's platonic-theological worldview. Yet, it is this heterogeneity of idealistic-morphological theories that serves as evidence for our claim that pure typology is simply an instrument of morphological generalisations, which contains no immanent directives for incorporating these generalisations into more inclusive theoretical constructs.

The latter is true also for philosophical concepts such as essentialism. Typology itself does not include constraints on the possible number of types, their fixedness, or on the character of their boundaries. Such constraints are due to peripheral concepts, which can include essentialism as a theoretical element.

The general methodology, philosophical background and scientific practices of "typological thinking" (as described for idealistic morphology) posed no immanent threat to the Synthesis and "population thinking". The typological methodology was organised in such a way that a *direct* clash of typology with any kind of causal theory was impossible. It was "peripheral" concepts that actually came into conflict with the growing Synthetic movement.

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References

- Amundson, R., 2005. *The Changing Role of the Embryo in Evolutionary Thought*. Cambridge University Press, Cambridge.
- Berg, L.S., 1926. *Nomogenesis or Evolution Determined by Law*. Constable, London.
- Birstein, V.J., 2001. *The Perversion of Knowledge: The True History of Soviet Science*. Westview Press, Cambridge, MA.
- Braun, A., 1862. Rede zur Feier des acht und sechzigsten Stiftungstages des medicinisch-chirurgischen. Friedrich-Wilhelms-Institutes, Berlin.
- Breidbach, O., 2001. Transformation statt Reihung: Naturdetail und Naturganzes in Goethes Metamorphosenlehre. In: Breidbach, O., Ziche, P. (Eds.), *Naturwissenschaften um 1800*. Hermann Böhlaus Nachf, Weimar, pp. 47–64.

- Breidbach, O., 2002. The former synthesis – some remarks on the typological background of Haeckel's ideas about evolution. *Theory Biosci.* 121, 280–296.
- Breidbach, O., 2003. Post-Haeckelian comparative biology – Adolf Naef's idealistic morphology. *Theory Biosci.* 122, 174–193.
- Breidbach, O., Ghiselin, M.T., 2002. Lorenz Oken and Naturphilosophie in Jena, Paris and London. *Hist. Philos. Life Sci.* 24, 219–247.
- Chung, C., 2003. On the origin of the typological/population distinction in Ernst Mayr's changing views of species, 1942–1959. *Stud. Hist. Philos. Biol. Biomed. Sci.* 34, 277–296.
- Claßen-Bockhoff, R., 2001. Plant morphology: the historic concepts of Wilhelm Troll, Walter Zimmermann and Agnes Arber. *Ann. Bot.* 88, 1153–1172.
- Claßen-Bockhoff, R., 2005. Aspekte, Typifikationsverfahren und Aussagen der Pflanzenmorphologie. In: Harlan, V. (Ed.), *Wert und Grenzen des Typus in der botanischen Morphologie*. Martina Galunder Verlag, Nümbrecht, pp. 31–52.
- Coleman, W., 1976. Morphology between type concept and descent theory. *J. Hist. Med.* 31, 149–175.
- Dacqué, E., 1904. Wie man in Jena naturwissenschaftlich beweist. Kielmann, Stuttgart.
- Dacqué, E., 1911. Paläontologie, Systematik und Deszendenzlehre. In: Abel, O., et al. (Eds.), *Die Abstammungslehre*. G. Fischer, Jena, pp. 169–197.
- Dacqué, E., 1915. Grundlagen und Methoden der Paläogeographie. G. Fischer, Jena.
- Dacqué, E., 1921. Vergleichende biologische Formenkunde der fossilen und niederen Tiere. Bornträger, Berlin.
- Dacqué, E., 1923. Biologie der fossilen Tiere. De Gruyter & Co, Berlin.
- Dacqué, E., 1927. Urwelt, Sage und Menschheit. Eine naturhistorisch-metaphysische Studie. Oldenbourg, München.
- Dacqué, E., 1932/33. Entwicklungslehre als anthropologisch-metaphysisches Problem. *Blätter Deut. Philos.* 6, 75–93.
- Dacqué, E., 1935. Organische Morphologie und Paläontologie. Bornträger, Berlin.
- Di Gregorio, M.A., 1995. A wolf in sheep's clothing: Carl Gegenbaur, Ernst Haeckel, the vertebral theory of the skull, and the survival of Richard Owen. *J. Hist. Biol.* 28, 247–280.
- Dobzhansky, Th., 1950. Human diversity and adaptation. *Cold Spring Harb. Symp. Quant. Biol.* 15, 385–400.
- Gleißner, P., 2005. Was ist das: ein Typus. In: Harlan, V. (Ed.), *Wert und Grenzen des Typus in der botanischen Morphologie*. Martina Galunder Verlag, Nümbrecht, pp. 53–80.
- Goethe, J.W. von, 1790a. Tag- und Jahreshefte. Als Ergänzung meiner sonstigen Bekenntnisse. In: Goethe, J.W. von, *Poetische Werke. Autobiographische Schriften*. Berliner Ausgabe, vol. 16, second ed. Aufbau-Verlag, Berlin, Weimar, pp. 6–330.
- Goethe, J.W. von, 1790b. Herzoglich Sachsen-Weimarischen Geheimraths Versuch die Metamorphose der Pflanzen zu erklären. Carl Wilhelm Ettinger, Gotha.
- Goethe, J.W. von, 1932. Goethes morphologische Schriften. In: Troll, W. (Ed.), *Sonderausgabe. Eugen Diederichs, Jena*.
- Hagemann, W., 1975. Eine mögliche Strategie der vergleichenden Morphologie zur phylogenetischen Rekonstruktion. *Bot. Jahrb. Syst.* 96, 107–124.
- Heberer, G. (Ed.), 1943. Die Evolution der Organismen. Ergebnisse und Probleme der Abstammungslehre. G. Fischer, Jena.
- Hoßfeld, U., 2001. Im 'unsichtbaren Visier': Die Geheimdienstakten des Genetikers Nikolaj V. Timofëeff-Ressovsky. *Medizinhistorisches J.* 36, 335–367.
- Hoßfeld, U., Olsson, L., 2002. From the Modern Synthesis to Lysenkoism, and back? *Science* 297, 55–56.
- Huxley, J., 1942. *Evolution: The Modern Synthesis*. Allen & Unwin, London.
- Jepsen, G.L., Mayr, E., Simpson, G.G. (Eds.), 1949. *Genetics, Paleontology, and Evolution*. Princeton University Press, Princeton, NJ.
- Junker, T., 2004. Die zweite Darwinsche Revolution. Basiliken-Presse, Marburg.
- Junker, T., Hoßfeld, U., 2002. The architects of the evolutionary synthesis in national socialist Germany: science and politics. *Biol. Philos.* 17, 223–249.
- Kraus, O., Hoßfeld, U., 1998. 40 Jahre "Phylogenetisches Symposium" (1956–1997): eine Übersicht – Anfänge, Entwicklung, Dokumentation und Wirkung. *Jahrb. Gesch. Theor. Biol.* V, 157–186.
- Kuhn, O., 1981. Die Evolution. Ergebnisse und Probleme. Gebr. Geiselberger, Altötting.
- Levit, G.S., Meister, K., 2005. Goethes langer Atem: Die "methodologischen Ideologien" in der Deutschen Morphologie des 20. Jh. *Verh. zur Geschichte und Theorie der Biologie*. VWB, Berlin Bd. 12 (forthcoming).

- Levit, G.S., Hoßfeld, U., Olsson, L., 2004. The integration of Darwinism and evolutionary morphology: Alexej Nikolajevich Sewertzoff (1866–1936) and the developmental basis of evolutionary change. *J. Exp. Zool. (Mol. Dev. Evol.)* 302B, 343–354.
- Levit, G.S., Hoßfeld, U., Olsson, L., 2005. From the “Modern Synthesis” to Cybernetics: Ivan Ivanovich Schmalhausen (1884–1963) and his research program for a synthesis of evolutionary and developmental biology. *J. Exp. Zool. (Mol. Dev. Evol.)* forthcoming.
- Mayr, E., 1959. Darwin and the evolutionary theory in biology. In: *Evolution and Anthropology: A Centennial Appraisal*. Anthropological Society of Washington, Washington, DC, pp. 409–412.
- Mayr, E., 1963. *Animal Species and Evolution*. Harvard University Press, Cambridge, MA.
- Mayr, E., 1980. Some thoughts on the history of the evolutionary synthesis. In: Mayr, E., Provine, W.B. (Eds.), *The Evolutionary Synthesis: Perspectives on the Unification of Biology*. Harvard University Press, Cambridge, London, pp. 1–48.
- Mayr, E., 1982. *The Growth of Biological Thought*. Belknap Press, Cambridge, London.
- Mayr, E., 1991. *One Long Argument. Charles Darwin and the Modern Evolutionary Thought*. Harvard University Press, Cambridge, MA.
- Mayr, E., 1996. The autonomy of biology. *Q. Rev. Biol.* 71, 97–106.
- Mayr, E., 1997. *Evolution and the Diversity of Life*. The Belknap Press of Harvard University Press, Cambridge, London.
- Mayr, E., 1999. Thoughts on the evolutionary synthesis in Germany. In: Junker, Th., Engels, E.-M. (Eds.), *Die Entstehung der Synthetischen Theorie: Beiträge zur Geschichte der Evolutionsbiologie in Deutschland*. VWB-Verlag, Berlin, pp. 19–30.
- Mayr, E., 2001a. The philosophical foundations of Darwinism. *Proc. Am. Philos. Soc.* 145, 488–495.
- Mayr, E., 2001b. *What Evolution Is*. Basic Books, New York.
- Mayr, E., Linsley, E.G., Usinger, R.L., 1953. *Methods and Principles of Systematic Zoology*. McGraw-Hill, New York.
- Meister, K., 2005a. Metaphysische Konsequenz. – Die Idealistische Morphologie Edgar Dacqués. *Neues Jah. Geol. Paläontol. Abhandlungen* 235, 197–233.
- Meister, K., 2005b. Wilhelm Troll (1897–1978) – Tradierung Idealistischer Morphologie in den deutschen botanischen Wissenschaften des 20. Jahrhunderts. *Hist. Philos. Life Sci.* (forthcoming).
- Meister, K., 2005c. Alternative Synthese in einer „Kritischen Biologie“? – Die Idealistische Morphologie Adolf Naefs. *Verhandlungen Gesch. Theor. Biol.* (forthcoming).
- Meister, K., 2006. Anti-Darwinismus in der Paläontologie des 20. Jahrhunderts – Die Idealistische Morphologie Oskar Kuhns (1908–1990). *Jahrb. Europäische Wissenschaftskultur* 2 (forthcoming).
- Naef, A., 1911a. Studien zur generellen Morphologie der Mollusken (Teil 1). *Erg. Fortschr. Zool.* 3, 73–164.
- Naef, A., 1911b. Studien zur generellen Morphologie der Mollusken (Teil 3). *Erg. Fortschr. Zool.* 6, 27–124.
- Naef, A., 1913. Studien zur generellen Morphologie der Mollusken (Teil 2). *Erg. Fortschr. Zool.* 3, 329–463.
- Naef, A., 1917. *Die individuelle Entwicklung organischer Formen als Urkunde ihrer Stammesgeschichte*. G. Fischer, Jena.
- Naef, A., 1919. *Idealistische Morphologie und Phylogenetik*. G. Fischer, Jena.
- Naef, A., 1923a. *Die Cephalopoden: Fauna und Flora des Golfes von Neapel*, vol. I. W. Engelmann Verlag, Leipzig.
- Naef, A., 1923b. Über systematische Morphologie und ihre Bedeutung für die Wissenschaft und Lehre vom Leben. *Vierteljahresschr. Naturforsch. Gesellsch. Zürich* 68, 387–397.
- Naef, A., 1931. Phylogenie der Tiere. In: Baur, E., Hartmann, M. (Eds.), *Handbuch der Vererbungswissenschaft*, Band 3. Bornträger, Berlin.
- Nickel, G., 1996. Wilhelm Troll (1897–1978). Eine Biographie. *Acta Hist. Leopoldina* 25.
- Nisbet, Ch., 1900. Annals; or day and year papers. In: Oxenford, J. (Ed.), *Bohn's Standard Library, Goethe's Works. The Autobiography of Goethe: Truth and Poetry from my own Life*. Books XIV–XX. Translated from the German, vol. II. George Bell and Sons, London.
- Reif, W.-E., 1986. The search for a macroevolutionary theory in German palaeontology. *J. Hist. Biol.* 19, 79–130.
- Reif, W.-E., 1993. Afterword. In: Schindewolf, O. (Ed.), *Basic Questions in Palaeontology*. University Press, Chicago, pp. 435–453.
- Reif, W.-E., 1997. Typology and the primacy of morphology: the concepts of O.H. Schindewolf. *Neues Jahrb. Geol. Paläontol.* 205, 355–371.

- Reif, W.-E., 1998. Adolf Naef's Idealistische Morphologie und das Paradigma typologischer Makroevolution. In: Engels, E.-M., Weingarten, M. (Eds.), *Ethik der Biowissenschaften*. VWB-Verlag, Berlin, pp. 411–424.
- Reif, W.-E., Junker, T., Hoßfeld, U., 2000. The synthetic theory of evolution: general problems and the German contribution to the synthesis. *Theory Biosci.* 119, 41–91.
- Remane, A., 1956. Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik, second ed. Geest & Portig, Leipzig.
- Rensch, B., 1947. Neuere Probleme der Abstammungslehre. Die Transspezifische Evolution. Ferdinand Enke, Stuttgart.
- Rensch, B., 1980. Historical development of the present synthetic Neo-Darwinism in Germany. In: Mayr, E., Provine, W. (Eds.), *The Evolutionary Synthesis*. Harvard University Press, Cambridge, MA, pp. 284–303.
- Richardson, M.K., Minelli, A., Coates, M.I., 1999. Some problems with typological thinking in evolution and development. *Evol. Dev.* 1 (1), 5–7.
- Schindewolf, O.H., 1927. Prinzipienfragen der biologischen Systematik. *Palaeontol. Zeitschr.* 9, 122–169.
- Schindewolf, O.H., 1936. Paläontologie, Entwicklungslehre und Genetik: Kritik und Synthese. Bornträger, Berlin.
- Schindewolf, O.H., 1947. Fragen der Abstammungslehre, Aufsätze und Reden der senckenbergischen naturforschenden Gesellschaft 1. Kramer, Frankfurt.
- Schindewolf, O.H., 1950. Grundlagen der Paläontologie. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.
- Schindewolf, O.H., 1952. Evolution vom Standpunkt eines Paläontologen. *Eclogae Geol. Helv.* 45, 375–386.
- 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. Mohr, Tübingen.
- Schindewolf, O.H., 1962. Neue Systematik. *Palaeontol. Zeitschr.* 36, 59–78.
- Schindewolf, O.H., 1969. Über den "Typus" in morphologischer und phylogenetischer Biologie. Akademie der Wissenschaften und der Literatur, Mainz.
- Schmalhausen, I.I., 1939. Die wissenschaftliche Tätigkeit A.N. Sewertzoffs als Theoretiker der Evolutionslehre. In: Schmalhausen, I.I. (Ed.), *À la mémoire de A.N. Sewertzoff*. AN USSR, Moscow-Leningrad.
- Schmalhausen, I.I., 1946a. Problemy Darwinizma (Problems of Darwinism). Sovetskaja Nauka, Moscow.
- Schmalhausen, I.I., 1946b. Faktory Evoljuzii (Factors of Evolution). AN SSSR, Moscow-Leningrad.
- Sewertzoff, A.N., 1949. *Sobranije sočinenij*, vol. 5. Izd. Akad. Nauk, Moscow.
- Starck, D., 1965. Vergleichende Anatomie der Wirbeltiere von Gegenbaur bis heute. Verhandlungen der Deutschen Zoologischen Gesellschaft in Jena, pp. 51–67.
- Troll, W., 1925. Gestalt und Gesetz. *Flora N.F.* 18/19, 536–565.
- Troll, W., 1928. Organisation und Gestalt im Bereich der Blüte. In: Beneke, W., Seybold, A., Sierp, H., Troll, W. (Eds.), *Monographien aus dem Gesamtgebiet der wissenschaftlichen Botanik 1*. Springer, Berlin.
- Troll, W., 1937. Vergleichende Morphologie der höheren Pflanzen 1, Teil 1. Bornträger, Berlin.
- Troll, W., 1939. Vergleichende Morphologie der höheren Pflanzen 1, Teil 2. Bornträger, Berlin.
- Troll, W., 1941. Gestalt und Urbild. Gesammelte Aufsätze zu Grundfragen der organischen Morphologie. In: Pinder, W., Troll, W., Wolf, L. (Eds.), *Die Gestalt 2*. Becher & Erler, Leipzig.
- Troll, W., 1943. Vergleichende Morphologie der höheren Pflanzen 1, Teil 3. Bornträger, Berlin.
- Troll, W., 1951. Biomorphologie und Biosystematik als typologische Wissenschaften. *Stud. Gen.* 4, 367–389.
- Troll, W., 1952. Über die Grundlagen des Naturverständnisses. *Scientia* 46, 11–18.
- Troll, W., 1964. Die Infloreszenzen. Typologie und Stellung im Aufbau des Vegetationskörpers, vol. 1. G. Fischer, Stuttgart.
- Troll, W., 1969. Die Infloreszenzen. Typologie und Stellung im Aufbau des Vegetationskörpers, vol. 2. G. Fischer, Stuttgart.
- Troll, W., 1971. Vergleichende Morphologie der höheren Pflanzen, vol. 1 (Suppl.). Bornträger, Berlin.
- Weberling, F., 1981. Wilhelm Troll. *Berichte Deutsch. Bot. Gesellsch.* 94, 311–324.
- Winsor, M.P., 2003. Non-essentialist methods in pre-Darwinian taxonomy. *Biol. Philos.* 18, 387–400.
- Zimmermann, W., 1953. *Evolution. Die Geschichte ihrer Probleme und Erkenntnisse*. Alber, Freiburg, München.
- Zündorf, W., 1940. Phylogenetische oder Idealistische Morphologie? *Der Biologe* V, 10–24.