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ORIGINAL PAPER

The "Biogenetic Law" in zoology: from Ernst Haeckel's formulation to current approaches

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Abstract 150 years ago, in 1866, Ernst Haeckel published a book in two volumes called "Generelle Morphologie der Organismen" (General Morphology of Organisms) in which he formulated his biogenetic law, famously stating that ontogeny recapitulates phylogeny. Here we describe Haeckel's original idea and follow its development in the thinking of two scientists inspired by Haeckel, Alexei Sewertzoff and Adolf Naef. Sewertzoff and Naef initially approached the problem of reformulating Haeckel's law in similar ways, and formulated comparable hypotheses at a purely descriptive level. But their theoretical viewpoints were crucially different. While Sewertzoff laid the foundations for a Darwinian evolutionary morphology and is regarded as a forerunner of the Modern Synthesis, Naef was one of the most important figures in 'idealistic morphology', usually seen as a type of anti-Darwinism. Both Naef and Sewertzoff aimed to revise Haeckel's biogenetic law and came to comparable conclusions at the empirical level. We end our review with a brief look at the present situation in which molecular data are used to test the "hour-glass model", which can be seen as a modern version of the biogenetic law.

Keywords Ontogeny · Phylogeny · Heterochrony · Atavisms · Homeobox

> "Perhaps I ought to explain", added the badger, lowering his papers nervously and looking at the Wart over the top of them, "that all embryos look very much the same". They are what you are before you are born—and, whether you are going to be a tadpole or a peacock or a cameleopard or a man, when you are an embryo you just look like a peculiarly repulsive and helpless human being".
> Terence H. White, The Once and Future King, 1958

Introduction

It is now 150 year ago that the German zoologist Ernst Haeckel (1834–1919 Fig. 1) published his first major scientific work, "General Morphology of Organisms", in 1866. Here he for the first time started to formulate his Biogenetic law, which he later developed further in a monograph on calcareous sponges ("Die Kalkschwämme") in 1872. Neither "Generelle Morphologie" nor "Die Kalkschwämme" were ever translated into other languages, and reached a limited audience even in the German-speaking lands. The popularisation of Haeckels ideas followed in 1868 when a collection of lectures that he had held at Jena University (where he was the first professor of zoology) were published as "Natürliche Schöpfungsgeschichte" (Natural History of Creation). This

Dedicated to the memory of Olaf Breidbach.

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popular science book became a bestseller and was also translated into many different languages.

How did Ernst Haeckel get the idea to write a very large monograph at this relatively early stage in his career? Clearly he wanted to revolutionize biology by using Charles Darwin's recently published evolutionary theory (or theories) as the foundation for this science. He had also secured a professorship and could start to lay out a long-term research program (as we would say today). The immediate reason for sitting down to write this massive work was—at least in part—personal or even private. The historian of biology Robert J. Richards has argued, in "The tragic sense of life", his biography of Haeckel (Richards 2008), that the effort that went into producing this enormous work, a book of almost 1000 pages published in two volumes, was connected with his reaction to the death of his first wife, Anna Sethe, from puerperal fever shortly after having delivered a daughter. On the day Richards interprets as the most important in Haeckel's life, February 16, 1864, he turned 30, received a prize for his scientific work (the Cothenius medal, Leopoldina Academy), and lost his wife. After this, Haeckel went into a frenzy of work, and completed the *General Morphology* within a year. Although he remarried, and took several lovers, nothing and no one could replace his beloved Anna.

The *General morphology of Organisms* (1866) consists of a first volume called "The general anatomy of organisms" (Allgemeine Anatomie der Organismen) and a second volume called "General developmental history" (Allgemeine Entwicklungsgeschichte). The subtitle is "General principles of the organic form-science, founded mechanically through the theory of descent as reformed by Charles Darwin" (Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformierte Descendenz-Theorie) The first volume was dedicated to Haeckel's teacher, the anatomist Carl Gegenbaur, and the second volume to the "founders of the theory of descent", Darwin, Goethe and Lamarck. This book is the key to Haeckels later work, its goal being to apply Darwin's theory to biology in general, but especially to morphology. Haeckel goes through both the animal and the plant kingdoms, concentrating on morphology and phylogeny (Niklas et al. 2016; Kutschera 2016). He coins new concepts for new avenues of research, and some of his many terms are still in use, such as ecology, phylogeny, ontogeny, and phylum. Haeckel also presents his first ideas on the relationship between ontogeny and phylogeny and introduces a system of the existing groups of organisms based on genealogy rather than the old typological and idealistic ideas (Hoßfeld 2010; Hoßfeld et al. 2016).

Another important aspect of the book is Haeckel's attempt to establish a promorphology—a general theory of basic forms—in the first volume. The second volume can be seen as a first attempt to establish evolutionary morphology and evolutionary embryology as new fields of research (Olsson et al. 2009a, b). In the seventh book, Haeckel also formulated his ideas for a biological anthropology based on Darwin's theory of evolution (Hoßfeld 2016a).

Ernst Haeckel choose the tree as a model for the depiction of natural relationships between organisms (Hoßfeld et al. 2016). The root symbolizes a common primordial form or ancestor, from which all other forms emerge. Haeckel writes that the "natutal systems of organisms is their natural genealogical tree", that is based on paleontological, embryological and systemic data, the so-called "threefold parallelism" that was so important to Ernst Haeckel's thinking. In the *Generelle Morphologie* he published eight phylogenetic trees and divided all living organisms into three kingdoms—animals, plants and protists (Hoßfeld 2010, 2016b; Hoßfeld et al. 2017).

Haeckel thought that evolution affected everything from inorganic matter to man, and believed in the unity of and the unity of spirit, philosophy and matter (monism is a philosophical system). This monism guided Haeckel's work from the *Generelle Morphologie* to his last book on "Crystal souls" (Haeckel 1917).

Because the *Generelle Morphologie* did not become the success that Haeckel had hoped for, he arranged for his successful Darwin lectures, attended by 200 students in the winter semester of 1867/68 (a third of all students at Jena University at the time) to be stenographed and later

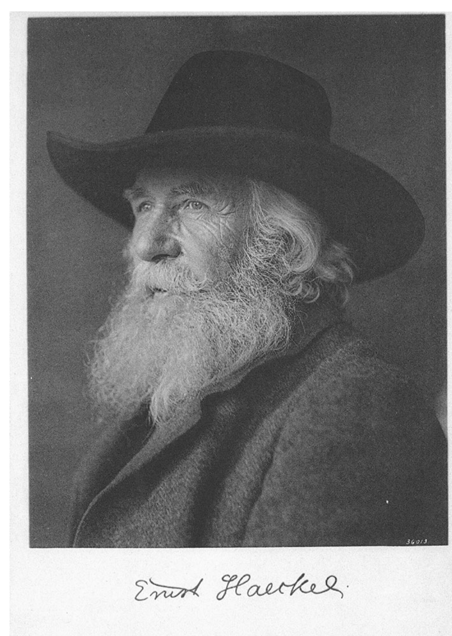

Fig. 1 Ernst Haeckel (1834–1919). Bildarchiv, Ernst-Haeckel-Haus, Jena

published as *Natürliche Schöpfungsgeschichte* in 1868 (translated as "The History of Creation" in 1876). Here he also made some revisions beased on the criticism he had received from Carl Gegenbaur (1826–1903) und Thomas H. Huxley (1825–1895). This book was written in a accessible style and, together with the *Anthropogenie oder Entwickelungsgeschichte des Menschen* from 1874 (English translation "*Anthropogeny: Or, the Evolutionary History of Man*", became a great success. It was translated into many languages and sold extremely well, and made an important contribution to the popularization of the theory of evolution in Europe and beyond (Hoßfeld and Olsson 2003; Williams 2006).

The biogenetic law: more then just embryology?

Having finished the *Generelle Morphologie*, Ernst Haeckel went on a trip to the Canary islands for several months. He did not seem interested in the reactiosn of his colleagues to his, sometimes very polemical, statements in the book. In a letter to Thomas H. Huxley from May 12, 1867 he notes that: "A radical reform of science […] cannot be undertaken by gently and soft, but only by energetic and reckless means" (Krauße 1984, our translation).

Ernst Haeckel succeeded in showing that anatomy and morphology, as well as developmental biology, could provide important data supporting the theory of descent. Just like Johann Friedrich Meckel the Younger (1781–1833) before him, Haeckel was convinced of the importance of the "parallelism" between comparative anatomy and development, between the anatomical changes over geological time and the changes during development of the embryo. Haeckel called the explanation for this parallelism the "The fundamental law of organic development, or in short form the 'biogenetic law". Haeckel wrote about the reciprocal causal relationships in his *Generelle Morphologie der Organismen*:

> 41. Ontogenesis is the short and fast recapitulation of phylogenesis, controlled through the physiological functions of inheritance (reproduction) and adaptation (nutrition).
>
> 42. The organic individual […] recapitulates through its fast and short individual development the most important of the changes in form, which the ancestors have gone through during the slow and long palaeontological development following the rules of inheritance and adaptation (Haeckel 1866, II: 300).

But Haeckel was well aware of the limitations and problems with his approach. He writes that:

> 43. The true and complete repetition of phyletic development by bionic development is reduced and shortened by secondary condensation, since ontogeny strikes out on an ever straighter course. Thus, the longer the sequence of successive juvenile stages, the more true will be the repetition (Haeckel 1866, II: 300).

In addition Haeckel states:

> 44. The true and complete repetition of phyletic development by biontic development is falsified and changed by secondary adaptation, since the bion adapts to new conditions during its individual development. Thus, the more alike the conditions of existence under which the bion and its ancestors have developed, the more true will be the repetition (Haeckel 1866, II: 300).

He later coined the terms *Cenogenie* (secondary adaptation) and *Palingenie* (true recapitulation) (Haeckel 1875; Grell 1979). Haeckel developed and applied his biogenetic law further as the "Gastraea theory" in his 1872 book on calcareous sponges. The Gastraea is a hypothetical primordial form ("Urform") common to all multicellular animals. Haeckel writes that the Gastraea cannot be found in the fossil record but can be reconstructed from the appearence of a gastrula stage in the embryonic development of most extant animals:

> From these identical gastrulae of representatives of the most different animal phyla, from poriferans to vertebrates, I conclude, according to the biogenetic law, that the animal phyla have a common descent from one unique unknown ancestor, which in essence was identical to the gastrula: Gastraea (Haeckel 1872, 1: 467).

Haeckel also illustrated gastrulation in different animals in his *Anthropogenie* (1874, Fig. 2). But the Gastraea theory did not follow by logical necessity from the data available to Haeckel. The Russian scholars Alexander Kowalevsky (1840–1901) and Elias (Ilya) Metschnikoff (1945–1916) worked along comparable lines. Haeckel appreciated Kowalevsky's work highly. In his *Anthropogenie* Haeckel wrote: "The most significant germ histories in the recent time were those of Kowalevsky" (Haeckel 1874, p. 49). It is astonishing in this respect that both Kowalevsky and Metschnikoff were hostile towards Haeckel's Gastraea theory. This is even more curious considering that Kowalevsky's younger brother Vladimir (1843–1883) made his doctoral work under Haeckel's supervision (Uschmann 1956) and that the Gastraea theory was to a significant extent based on Kowalevsky's data. Metschnikoff (1876, quoted from: Gourko et al. 2000,

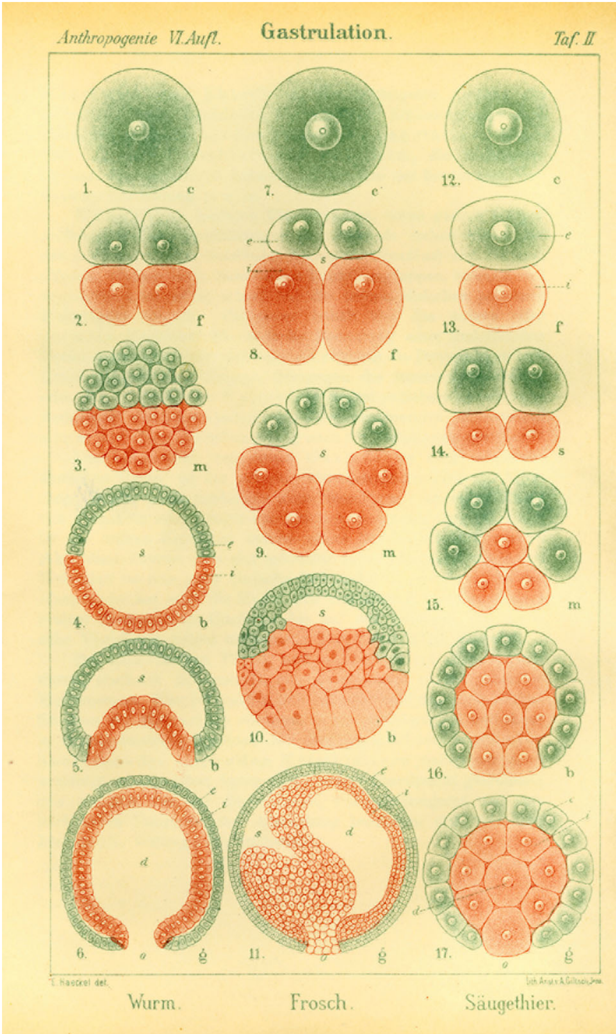

Fig. 2 Gastrulation in different animals. In: Haeckel, E. (1874) Antropogenie

p. 90) was straightforward in his verdict on Haeckel's theory: "As often happens, when a great scientist is hesitant to draw a crucial conclusion because of insufficient evidence, this claim is made by a less careful dilettante. In our case this role is played by Haeckel with his Gastraea theory. Everything really valuable and scientifically proven in this theory belongs to others, mostly to Kovalevsky". Due to his work with *Coelenterata* (*Cnidaria* and *Ctenophora*) Kowalevsky was very aware that gastrulation by ingression is as possible as by invagination, and that Haeckel's theory is hardly applicable to the developmental processes in hydroid polyps. Kowalevsky admitted alternative ways of gastrulation (Levit 2007).

Yet, Haeckel was convinced that with his Gastraea theory he had proved the monophyletic origin of all multicellular animals. If the two primary germ layers really are homologous in all metazoans, as Haeckel postulated, then he had given an evolutionary explanation of this early and important embryological process, the origin of germ layers (Haeckel 1874, 1875; Grell 1979; Niklas et al. 2016).

The theory of evolution and the "Biogenetic Law"

> "I bought the pig immediately, had it killed and the feet hacked off, and sent them to Darwin"[1]

The journalist and plankton researcher Otto Zacharias (1846-1916) was an important popularizer of Haeckel's "Darwinismus" and corresponded with Haeckel throughout the last quarter of the nineteenth century (Nöthlich et al. 2006). The quotation above illustrates the importance of Haeckel's so-called biogenetic law for discussions about evolution in this era. In a letter from 1877, Zacharias describes how he came across, at the local marketplace, a pig with "thumbs", which are normally completely absent, developed on both forelimbs. Such atavistic mutations, which bring forth characters that have long been lost in the evolutionary line leading to an extant species, were seen as "throwbacks" to earlier eras, and as important evidence for evolution as descent with modification. So excited was Zacharias by this discovery, that he bought the pig, and after it had been slaughtered and the forelimbs "hacked off", sent at least one of the pigs feet to Charles Darwin and asked for his comments on the phenomenon and its importance for the theory of evolution. Darwin sent the foot to the anatomist W. H. Flower in London and wrote: "The pigs-foot has been dispatched to day per Rail" on May 2, 1877. Flower made a thorough investigation and wrote back to Zacharias that he had seen similar examples before, but this was an unusually well developed "pigs thumb".

Why did atavisms provoke such interest and enthusiasm in those days? An *atavism* is defined as the reappearance in a member of an extant species of a character that has been lost during phylogenesis, such as hind legs in whales or teeth in birds. The direct cause might be that a developmental program that is normally not active in this species has been re-activated. In a classic paper, Brian Hall (1984, and see also Hall 1995) has reviewed the developmental basis of atavisms. The biogenetic law could take atavisms into account without problems. They were just re-appearances of characters that this species had once possessed during its phylogenesis. That such characters could appear in its present ontogenesis was in accordance with "ontogeny recapitulats phylogeny".

[1] German original: „Ich acquirierte das Schwein sofort, ließ dem Niederstechen die Pfoten Abhacken u. schickte dieselben an Darwin". Courtesy: Otto Zacharias in a letter to Ernst Haeckel, 21 May, 1877; Archive of the Ernst-Haeckel-House in Jena, correspondence Haeckel.

Also Darwin himself pointed out the importance of embryology for revealing community of descent. He put great value on this relationship for systematics (Darwin 1871, 1: 205). Maybe the most important contribution to discussing Haeckel's biogenetic law critically was Fritz Müller's book "Für Darwin" (1864). Müller studied crustaceans and came to the conclusion that evolutionary changes take place mostly through "Abirren" (literally, going astray, here divergence from the original developmental pathway) and "Hinausschreiten" (literally, transgression, here development beyond the endpoint of the original developmental pathway). Thus Müller explained phylogenetic changes by reference to changes in ontogeny, while Haeckel did the opposite—in phylogeny he saw the explanation for ontogeny. The goals were also different. While Müller sought causal explanations, Haeckel erected a law based on his observations and preconceived ideas (Breidbach and Ghiselin 2008).

The discussions surrounding the biogenetic law exemplify the fertile interaction between embryology and comparative anatomy in the nineteenth century (Hoßfeld et al. 2003). They also show that ontogenetic results must be used with caution in evolutionary biology. When the concepts and terminology introduced by Haeckel did not suffice to answer the questions at hand, several biologists tried to supplement or replace the biogenetic law. These discussions became important milestones in the history of evolutionary developmental biology (Olsson and Hoßfeld 2007; Hoßfeld and Olsson 2008; Olsson et al. 2010).

Here we will concentrate on two scientists which developed the biogenetic law in important ways, Alexej N. Sewertzoff (1866–1936) and Adolf Naef (1883–1943). Sewertzoff had his major influence in the Russian- and German-speaking lands, and his theory was arguably the most fundamental and radical revision of Haeckel's biogenetic law in the first decades of the twentieth century. Less influential was the theory of the advocate of idealistic morphology, Adolf Naef, who also coined this term. In the mid-1920s, during one of his visits at the *Stazione Zoologica di Napoli*, Naef had long discussions with Sewertzoff. There were, however, differences between their theories, and it is known that Sewertzoff based the empirical part of his theory to a large degree on the works of the Swedish paleontologist Erik Stensiö, whose work apparently did not influence the others (Olsson 2005). The differences and mutual influences of Naef's and Sewertzoff's theories have received little attention from historians of biology (but see Levit et al. 2015), although this is crucial for an understanding of the theoretical developments in evolutionary and developmental biology.

Alexej Sewertzoff's theory of Phylembryogenesis

Alexej Nikolajevich Sewertzoff (1866–1936, Fig. 3) laid the foundations for a strictly scientific evolutionary morphology by proposing a concept of progress free from teleology, and a radically revised recapitulation theory. His revised theory of how phylogeny and ontogeny are related contributed significantly to the development of selectionist thinking (Hoßfeld 2001; Levit et al. 2004; Hoßfeld and Levit 2012).

Inspired by his trip in 1925/26 to Weimar, Jena, Vienna, Munich, Göttingen and Naples, Sewertzoff began writing what is arguably his most important contribution to evolutionary biology, the monograph *Morphologische Gesetzmäßigkeiten der Evolution* (Sewertzoff 1931). The book was written in German and published by Gustav Fischer Verlag in Jena. Eight years later a Russian version, composed of an authorized translation made by his wife and some significant additions made by Sewertzoff himself, appeared (Sewertzoff 1939). Therefore the Russian version, which also appeared in a second edition ten years later (1949) is the most comprehensive representation of his ideas.

The core of Sewertzoff's theoretical system is the concept of phylembryogenesis. In its final form this concept was the result of more than twenty-five years of research into the phylogeny-ontogeny problem. The ideas and terminology of this theory are still presented in Russian textbooks, but otherwise relatively unknown, although Gould (1977) discussed them briefly in his classic *Ontogeny and Phylogeny*.

Sewertzoff's purpose was a radical revision of Haeckel's view on the relationships between ontogeny and phylogeny in order to rescue the very idea of recapitulation.

Fig. 3 A.N. Sewertzoff (1866–1936) in Moscow in 1915 (from the archive of the Sewertzoff family)

From his analysis of the history of the biogenetic law, it is clear that Sewertzoff thought very highly of Fritz Müller's approach to the problem of recapitulation. Müller had developed "his application of the recapitulation theory, thereby inspiring Haeckel's enthusiasm for the link between ontogeny and phylogeny" (Bowler 1996, 106). In Sewertzoff's opinion, Müller (1864, 74–81) had identified the problem very clearly: "It was F. Müller who proposed that evolutionary changes of the adult forms arise not only from the sum of variations of these forms (this is what Darwin, Haeckel and Weismann discussed), but proceed by means of *gradual alterations of embryonic and larval development*" (Sewertzoff 1949, 374). Haeckel argued that "phylogeny is the mechanical cause of ontogeny" (Haeckel 1874, 5) but neglected the idea of an evolutionary impact of ontogeny on phylogeny, which survived in Germany mostly in the works of adherents to orthogenesis, such as Albert von Kölliker (1817–1905), and in the works of the idealistic morphologist Adolf Naef. The theory of phylembryogenesis was along the same lines and represented, in a certain sense, a return to Müller's concept of recapitulation as opposed to Haeckel's biogenetic law (Severtzov 1970, 2012).

Sewertzoff himself acknowledged that he initially wanted to prove that recapitulation is the proper method for phylogenetic studies. Investigations had shown, however, that the recapitulation of ancestral features was not a universal phenomenon, and that it was detectable only in certain cases. This was in agreement with Sewertzoff's concept of progress, because according to his theory of phylembryogenesis the phylogenetically older forms are not necessarily more 'primitive' (Sewertzoff 1949, 381, 396). The phylembryogenesis theory assumes that deviations in the course of ontogenesis can cause changes in adult structures. Sewertzoff saw this idea in contrast to the concept of *coenogenesis*, during which embryonic adaptations do not affect the adult stages. As his student Schmalhausen comments:

> Phylembryogeneses are embryonic changes related to the phylogenetic development of the adult organism. Since every individual deviation is rooted in the process of ontogenetic development, the natural selection of such deviations inevitably results in the reorganisation of ontogenesis. The only question is at which stages and why these changes occur (Schmalhausen 1969, 357).

To answer this general question Sewertzoff distinguished three basic modes of phylembryogenesis: anaboly, deviation, and archallaxis.

Anaboly, *i.e.* changes to ontogeny by extension explains 'von Baer's law', which claims that features of the adult forms appear in a certain sequence during embryonic development, and that this sequence corresponds to the hierarchy of systematic categories (e.g. family-genus-species), to which the individual belongs. von Baer's law should not be confused with Haeckel's view of it, i.e. "the pressing back of adult ancestral stages into the young stages of the descendants" (de Beer 1932). Sewertzoff stressed the difference between 'von Baer's law' and Haeckel's recapitulation. He wrote that

> v. Baer's law shows us the order in which the characters which are present today in adult animals were established; the law of recapitulation shows us, on the contrary, the order in which the ancestral characters, which once were present in the adults of the ancestors of the discussed forms, but have been replaced by other characters in the recent adult animal, develop (Sewertzoff 1931, 278–279; 1949, 418).

Sewertzoff maintains that *morphogenesis* is a period lasting from the beginning of ontogeny to the stage at which an individual acquires its most characteristic features. Therefore anaboly can be defined as an extension of morphogenesis. The exact connection between von Baer's law and anaboly consists in that anaboly takes place when the last stages of morphogenesis of a certain organ, which are similar to the adult organ in the ancestor, are completed by the addition of new stages to ontogenesis (Sewertzoff 1931, 275). Hence, Sewertzoff argued, anaboly is the simplest, the slowest and phylogenetically the most basal mode of phylembryogenesis (Sewertzoff 1934).

Deviation is a departure from the usual course of ontogeny, which occurs in the middle stages. Sewertzoff adapted the term 'middle stage deviation' from Victor Franz (1927), although he knew that the same phenomenon had been described earlier by Adolf Naef (1917). In contrast to anaboly, 'middle stage deviation' does not extend morphogenesis.

Archallaxis. While deviation explains the phenomenon of partial recapitulation, archallaxis explains cases with no recapitulation at all. Briefly defined, archallaxis is an evolutionarily significant modification occurring during the earliest stages of ontogeny (Sewertzoff 1927). All three modes of phylembryogenesis exist in *positive* and *negative* forms. The negative form of anaboly is the deletion of the last stage of ontogeny (as opposed to its extension). Negative deviation and negative archallaxis mean the regress of primordia in the middle or early stages of embryonic development, respectively (Sewertzoff 1949, 402).

The evolution of a certain feature can combine various modes of phylembryogenesis. For example, a feature can, for a certain period, evolve by means of anaboly, but later convert to archallaxis. Sewertzoff labelled such cases as 'secondary archallaxis'. Likewise, various features of the organism can evolve by different modes.

In summary, the theory of phylembryogenesis separated the problem of recapitulation from Haeckel's biogenetic law. Sewertzoff was convinced that the recapitulation of features of the adult ancestors cannot even in principle take place by 'middle stage deviation' and archallaxis. Therefore, recapitulation cannot be a reliable method for reconstructing phylogenies. At the same time phylembryogenesis—a comprehensive concept postulating variability at all stages of ontogeny—made it possible to integrate the ontogeny-phylogeny problem into the framework of Darwinian theory. Further work in Russia along these lines, attempting a synthesis of phylembryogenesis theory and evolutionary morphology with population genetics, was later performed mostly by Schmalhausen and his school.

Adolf Naef and his 'law of terminal modifications'

Sewertzoff viewed Adolf Naef (1883–1943) as someone who approached the problem in a way similar to his own. The reason was Naef's 'law of terminal modifications' (Naef 1917, 57). In Sewertzoff's view Naef came quite close to Fritz Müller's ideas. Although the same basic assumption that phylogeny is due to modified ontogeny was shared also by others, Sewertzoff paid special attention to Naef's version of the relationship between ontogeny and phylogeny.

Naef was one of the crucial figures in idealistic morphology. They called their science systematic morphology or comparative morphology (Rieppel 2011a, b). The so-called typological method was the foundation for their research programs. However, typology was only one element (although important) of their theoretical systems, which also included further elements, such as creationism, phylogeny, mutationism, orthogenesis, and neo-Lamarckism. All idealistic morphologists subscribed to the 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 (Levit and Meister 2006). In Germany the beginning of scientific morphology, and simultaneously of typology, is closely connected with Johann Wolfgang von Goethe (1749–1832), whose goal was to explain the structure of Nature as a whole (Niklas and Kutschera 2017). 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.

In the first part of the twentieth 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 the biological sciences in Germany (Meister 2005a; Levit and Meister 2005, 2006). Almost simultaneously, several biologists declared themselves to be adherents of typology. However, unlike the early typology, this new movement explicitly opposed their typological method to the method of evolutionary morphology. It was represented by Edgar Dacqué (1878–1945), Wilhelm Troll (1897–1978), Wilhelm Lubosch (1875–1938), Otto Heinrich Schindewolf (1896–1971), Adolf Remane (1898–1976) and many others, including Adolf Naef. At the same time, idealistic morphology was not a methodological monolith opposed to Darwinian evolutionary morphology, but rather a heterogeneous movement (Rieppel et al. 2013). The different idealistic morphologists had the basic principles of typology in common, but interpreted the results of typological classification differently. Naef tried to stay within the framework of the established empirical sciences and the pure typological method, without straying into metaphysical and almost religious generalisations in the manner of Troll or Dacqué (Meister 2005a, b).

Naef's primary scientific focus was on molluscs. His early work dealt with the biology of cephalopods. He saw it as his task to create a new synthesis (not to be confused with the Darwinian "Modern Synthesis"), i.e. to revise the foundations of morphology within the context of a broader theoretical perspective (Reif et al. 2000). His new morphology was to be built on the "sound foundation of old idealistic morphology" (Naef 1919, 13). Naef, as well as other idealistic morphologists found this 'sound foundation' in the works of Goethe. Naef's basic assumption was that the living world can be described as a hierarchical classification system organised according to increasing degrees of generality. He proposed that within this natural system more or less clearly definable units can be distinguished, which can be thought of 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 1923, 391). The method to use is comparative morphology, by which general features can be separated 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 1923, 390). The type, according to Naef, is a kind of mathematical abstraction, but it can also be (actually or potentially) manifested in a specific organism. The variation around a certain type, which he called the 'circle of forms' (Formenkreis), can be deduced logically. Naef's method was to first collect knowledge about the type inductively, and then deduce all possible forms. The sum total of the 'circles of forms' builds the foundation for a new systematics. Naef labelled his approach the 'new synthesis' or 'systematic morphology'. Systematic morphology brings order to the forms by describing their locations in the system as a whole. It is a descriptive science and Naef thought that 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 a proto-form in the simplest possible way, i.e. through the shortest morphogenesis. It is this form, derived from a comparison of many different structures, that 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, 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 an imaginary vertebrate" (Naef 1917, 17). Naef compared biological objects with crystal forms that fluctuate around certain reproducible mathematical abstractions, but rarely completely correspond to these abstractions. The 'old' synthesis was, according to Naef, created by Ernst Haeckel (Levit and Hoßfeld 2006):

> 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* (Naef 1917, 4) [our italics].

Because Naef saw the quintessence of Haeckel's research program in the biogenetic law, he subjected Haeckel's concept to significant revision. As Rieppel et al. (2013) put it: "Throughout his career, Naef was preoccupied with the critique and amendment of Haeckel's (1866) biogenetic law". In fact, Naef proposed a modernised form of it within the framework of his own morphological theory.

Naef's type is not a platonic idea but rather a scientific model without mystical features. His morphology is a *dynamic* theory of the relationship between ontogeny and phylogeny. 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, 24). Multicellular organisms develop by means of processes which Naef called 'morphogeneses'. Yet morphogeneses are based on germinal development, which is, again, of a rhythmic-cyclic nature. This dynamic approach allowed Naef to reformulate Haeckel's biogenetic law (Fig. 4).

Naef assumed that "the most general, and in its consequences most significant, fact derived from unbiased comparison of ontogeneses is this: the preliminary stages of homologous formations, i.e. the beginnings of morphogeneses, are always much more similar than they appear during their later phases" (Naef [1928] 2000, 17). But Naef interpreted these similarities in a characteristic typological way by claiming that "strong similarity of very early states is important not only as a foundation for the 'morphological primacy of ontogenetic precedence', it also facilitates (even for the unmethodical observer) obtaining an image of the primary type, i.e. of the ontogenetic norm valid within certain form ranges" (ibid.).

But what is the structure of Naef's concept of ontogenesis? Naef rejected the idea of "terminal lengthening of ontogenesis as proposed by F. Müller" (Naef [1928] 2000, 32) and thus Sewertzoff's anaboly. And he explicitly rejected any palingenesis which he found in the works of Sewertzoff (ibid., 340). Rejecting anaboly, Naef appealed to von Baer: "as has been shown already by K. E. v. Baer, ontogenetic stages in general do not represent adult stages of related, but lower animals; instead they correspond, often in a strikingly complete way, to homologous transitional stages of such lower relatives" (ibid., 25–26). Naef believed that the early stages of ontogenesis, showing a higher degree of generality, are "relatively conservative"

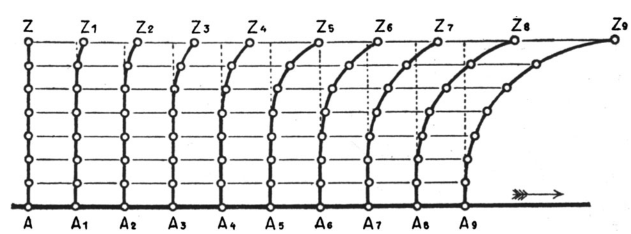

Fig. 4 Naef's "*law of terminal modification*". Haeckel's biogenetic law in Naef's interpretation (*left*) and Naef's own "law of terminal modification" (*right*). The vertical lines symbolize ontogenetic pathways. *Horizontal heavy lines* manifest the continuity of the development from one egg cell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

and therefore hardly suitable for Sewertzoff's theory of archallaxis. Without rejecting a theoretical possibility of important modifications of the early stages of ontogenesis, Naef believed that the tempo of heritable modification was lower for them than for later stages. Along these lines Naef proposed 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, 57).

So Naef's 'law of terminal modification' is not a negation, but rather a refinement of Haeckel's biogenetic law, which in its essence is similar to Sewertzoff's approach to ontogeny and phylogeny. 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 was especially effective for reconstructing large gaps in the fossil record. It is important to emphasize 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 2001, 286), it is evident that Naef's typology was *not* a kind of essentialism. We agree with Rieppel's (2011b, 9) claim that "evidently, there is no room for essentialism with respect to Naef's concept of a species specific type nor can Naef's type concept in general be considered essentialistic".

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 empirical work on the morphology and phylogeny of molluscs, especially cephalopods (Naef 1911, 1913). In later periods Naef worked on vertebrates, especially tetrapods (Naef 1931), and made significant inquiries into their embryology, an activity which was stimulated by the necessity to test his law of terminal modifications.

Naef vs. Sewertzoff

The idea of an evolutionary impact of ontogeny on phylogeny was important for both Naef and Sewertzoff (Kolchinsky 2014). This was a radical revision of Haeckel's biogenetic law, which claimed that phylogeny is a 'mechanical' cause of ontogeny, yet without proposing any detailed mechanism for their reciprocal influence. Sewertzoff's phylembryogenesis and Naef's terminal modifications are theories that outline various ways in which development can evolve and can be seen as forerunners to contemporary evo-devo (Hall 2000; Gilbert 2003). Sewertzoff's concept of archallaxis (which was later adapted by Schmalhausen), contributed significantly to the Darwinian (selectionist) interpretation of the tempo of evolution. But why did thinking along Darwinian lines enable Sewertzoff to be more radical than the idealistic morphologist Naef? Did Naef's typological background play any role in his discussions with Sewertzoff? The German paleontologist and historian of science Wolf-Ernst Reif has argued that although Naef's methodology formed a basis for a structuralist morphology, his results were potentially translatable into the language of Darwinian evolutionary morphology (Reif 1998).

We agree that a debate about the relative evolutionary importance of early vs. late stages of ontogenesis would be possible between two Darwinians as well and should not necessarily be interpreted in terms of a conflict between typology/essentialism and Darwinian population thinking. Yet, in the case of Naef, his typology played a significant role for his view that early stages of ontogenesis are more conservative than later stages. The reason for it is the epistemological objectives promoted by idealistic morphology. As Naef emphasized, a typologist initially looks for a purely intuitive picture of the typical, which appears in his "spiritual eye with internal necessity" (mit innerer Notwendigkeit) and only afterwards does a typologist elaborate scientific criteria for distinguishing typical from atypical (Naef 1931, 95). Naef always looked for the typical, whereas Sewertzoff's spiritual eye was free from the necessity to intuitively look for a norm. This methodological bias determined Naef's developmental biology to a significant extent and led to the discrepancy between his and Sewertzoff's revisions of Haeckel's biogenetic law. At the same time, the dynamic version of typology advocated by Naef allowed him to develop the idea of morphogeneses and urged him to reformulate Haeckel's biogenetic law. Naef and Sewertzoff lived in different theoretical worlds, but the very dynamism that Naef introduced to his concept "corrupted" the essentialist features of his idealistic morphology and brought him close to the pro-Darwinian evolutionism of Sewertzoff.

The Biogeneic law today

Today the concept of a phylotypic stage, a stage where all species belonging to the same phylum are morphologically very similar (like in Haeckel's embryo drawings), is often replaced by a "phylotypic period" (Rieppel 2016; Niklas et al. 2016). To illustrate this, the "hourglass model" (Levit and Hoßfeld 2011), initially proposed by Duboule (1994) and Raff (1996), is often used. In this model, the middle part is very narrow, symbolically interpreted as indicating that variation at the middle stages of development is very constrained. Earlier and later stages are more variable. Very early developmental stages can also look very different because of differences in yolk content and thereby egg size, whereas later stages are more variable because the embryo develops more and more of the characters seen in the adult animal. Unlike according to Haeckel's biogenetic law, similarities between embryos of different species within a phyllum are not considered to be caused by the recapitulation of former adult stages, but the causes a found on the molecular level (transcription factors, signaling pathways etc.).

Today new methods, such as transcriptome analysis (Levin et al. 2016), are used to test the validity of the hourglass model. It has been shown that animals show similar gene expression patterns at the phylotypic period, when they also look very similar (e.g. Kalinka et al. 2010; Domazet-Lošo and Tautz 2010). These molecular mechanisms, which are conserved within a phylum, can explain the morphological similarities (or Bauplan) and function as constraints that limit variation at the phylotypic stage (Irie and Kuratani 2014).

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