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Alexei Sewertzoff and Adolf Naef: revising Haeckel's biogenetic law

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Abstract Ernst Haeckel formulated his biogenetic law, famously stating that ontogeny recapitulates phylogeny, in 1872. The Russian evolutionist Alexei Sewertzoff, and the Swiss-born zoologist Adolf Naef were among those who revised Haeckel's law, thus changing the course of evolutionary theory and of developmental biology. Although Sewertzoff and Naef approached the problem in a similar way and formulated similar hypotheses at a purely descriptive level, 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", which is 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. This paper is an attempt to explain how their fundamentally different theoretical backgrounds influenced their views on the relationship between ontogeny and phylogeny.

Keywords Biogenetic law · Ernst Haeckel · Alexei Sewertzoff · Adolf Naef · Idealistic morphology · Evolutionary morphology

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1 Introduction

Soon after Darwin's major books appeared in print (Darwin 1859, 1871), Ernst Haeckel published his biogenetic law (Haeckel 1872), famously stating that ontogeny recapitulates phylogeny (Hossfeld and Olsson 2003). Haeckel was in his turn influenced by pre-Darwinian thinkers such as Karl Ernst von Baer, who had noted that the early developmental stages of different species showed similarities where no such similarities were observable in adults of these species. Haeckel put great theoretical emphasis on the parallel between the stages of development of the embryo, and the series from lower to higher forms of animals studied in comparative anatomy and systematics. He used the term *Entwickelung* for both the development of the individual and the development over evolutionary time. To these two parallels he added a third, based on paleontological data, namely the "development" of forms as seen in the fossil record, thus emphasising a threefold parallelism of phyletic (paleontological), biontic (individual), and systematic developments (Haeckel 1866, II, 371ff). He believed this threefold genealogical parallel represented "the fundamental law of organic development, or in short form the 'biogenetic law'". Haeckel wrote about the mutual causal relationship between ontogeny and phylogeny in his *Generelle Morphologie der Organismen* (General Morphology of Organisms):

> 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 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).

Haeckel was well-aware of the problems associated with the biogenetic law (Ulrich 1968; Uschmann 1966), since complete and faithful recapitulation is never observed in nature. Haeckel's views on both the mechanisms of evolution and the developmental processes remained contradictory. Furthermore, his "old-school Darwinism" (Levit et al. 2006) contained a strong neo-Lamarckian element. Haeckel's recapitulation theory was "essentially a Lamarckian rather than a Darwinian concept" (Bowler 1992, 84).

Haeckel's contemporaries were very critical towards his simplistic recapitulationism. For instance, it is well known that Haeckel based his biogenetic law primarily on Alexander Kowalevsky's (1840–1901) empirical studies. Haeckel himself claimed that "[t]he most significant germ histories in the recent time were those of Kowalevsky" (Haeckel 1874, 49). Kowalevsky and his closest friend and collaborator, Elie (Ilja) Metchnikov (1845–1916), a 1908 Nobel Laureate for his achievements in immunology, described ontogenies of many groups of invertebrates and lower chordates, and discovered homologies in early embryonic stages. They elaborated a universal theory of germ layers, declaring homology of the germ layers in all metazoa. Notwithstanding Haeckel's enthusiasm, both were actually rather critical towards his schematic and speculative embryology.

The Kowalevsky-Metchnikov idea of evolutionary plasticity of all stages of embryonic development, with a special emphasis on the role of the early stages of ontogenesis, was further developed in the works of the founder of the Russian school of evolutionary morphology Alexei N. Sewertzoff (1866–1936). Sewertzoff's theory was arguably the most fundamental and radical revision of Haeckel's biogenetic law in the first decades of the twentieth century. It was paralleled by some comparable, though not identical concepts developed in other national traditions. Foremost among these in the German-speaking countries was that developed by the zoologist Victor Franz (1883-1950). Franz was acquainted with Sewertzoff. He claimed to be the first person to have elaborated a theory of the differential impact of deviations (*Abänderung*—a departure from the usual course of ontogeny) on different stages of embryonic development—and subsequently on the course of phylogeny. Also involved in the debate was another very influential, now almost completely forgotten figure, the zoologist and geneticist Ludwig Plate (1862–1937) (Levit et al. 2006). Plate conducted genetic research on evolution and development trying to combine selectionist, Lamarckian and orthogenetic approaches. Less influential was the theory of 'idealistic morphology', a term coined by its advocate, Adolf Naef. He worked closely with Sewertzoff for a time and proposed a theory comparable to the concepts of both Franz and Sewertzoff. Naef held long discussions with Sewertzoff during one of his visits at the Stazione Zoologica di Napoli in the mid-1920s. There were differences between their theories. Sewertzoff was alone in basing the empirical part of his theory to a large degree on the works of the Swedish paleontologist Erik Stensiö (Olsson 2005). The differences and mutual influences of Naef's and Sewertzoff's theories have received little attention from historians of biology, although this is crucial for an understanding of the theoretical developments in evolutionary theory and developmental biology.

The present paper is an attempt to answer the question of how these researchers, using crucially different theoretical methodologies, could come to such similar conclusions on the necessity for a revision of Haeckel's biogenetic law. Though a fuller consideration of the parallels between the continental tradition in developmental biology and Anglo-American developments is beyond the scope of this paper, Sir Gavin de Beer (1899–1972), for example, proposed his revision of Haeckel's recapitulation theory. De Beer, like Franz and Naef, was well-acquainted with Sewertzoff's work, as testified by his voluminous and very favourable book review of Sewertzoff's *Morphologische Gesetzmässigkeiten der Evolution* in *Nature* (de Beer 1932).

2 Alexei Sewertzoff's theory of phylembryogenesis

Alexei Nikolajevich Sewertzoff (Fig. 1) 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.

Fig. 1 A.N. Sewertzoff in Moscow in 1915 (from the archive of the Sewertzoff family)

Sewertzoff had a major influence in the Russian- and German-speaking worlds (Hossfeld 2001). He belonged to a family of scientists, a family tradition which continues to the present day (Mirzoyan 1981; Levit et al. 2004). The founder had been Nikolaj Alexeevich Sewertzoff (1827–1885), a well-known Russian zoologist and geographer, a passionate traveller and adventurer, and one of the first biologists in Russia to actively propagate Darwinian ideas. He exerted a strong influence on his son, Alexei Nikolajevich Sewertzoff, who was thus "predestined" to become an evolutionary biologist.

Inspired by his trip in 1925–1926 to Weimar, Jena, Vienna, Munich, Göttingen and Naples, Sewertzoff began to write what was arguably his most important contribution to evolutionary biology, the monograph *Morphologische Gesetzmäßigkeiten der Evolution* (Morphological Regularities of Evolution, 1931), published by Gustav Fischer Verlag in Jena. Eight years later a Russian language version appeared, comprising an authorized translation made by his wife, and some significant additions made by Sewertzoff himself (Sewertzoff 1939). The first Russian version and the second edition (1949) are therefore the most comprehensive representation of his ideas.

The core of Sewertzoff's theoretical system is the concept of phylembryogenesis. In its final form the elaboration of this concept was the culmination of more than 25 years of research into the phylogeny-ontogeny problem. The ideas and terminology of this theory are still present in Russian textbooks, but quite unknown outside Russia, although Gould discussed them briefly in his classic *Ontogeny and Phylogeny* Gould (1977).

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. The first documented attempt to formulate the basics of his phylembryogenesis theory can be traced back to 1910, to his talk at the XII Congress of Russian naturalists and physicians (Sewertzoff 1910), whereas the term 'phylembryogenesis' was coined 2 years later (Sewertzoff 1912). From his analysis of the history of the biogenetic law, it is clear that Sewertzoff thought very highly of Fritz Müller's (1821–1897) 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 however argued that "phylogeny is the mechanical cause of ontogeny" (Haeckel 1874, 5), neglecting the idea of an evolutionary impact of ontogeny on phylogeny. This idea 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 developed 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). Instead, deviations in the course of ontogenesis could 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 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 or prolongation, for Sewertzoff, involved the addition of new stages at the end of a period of form development

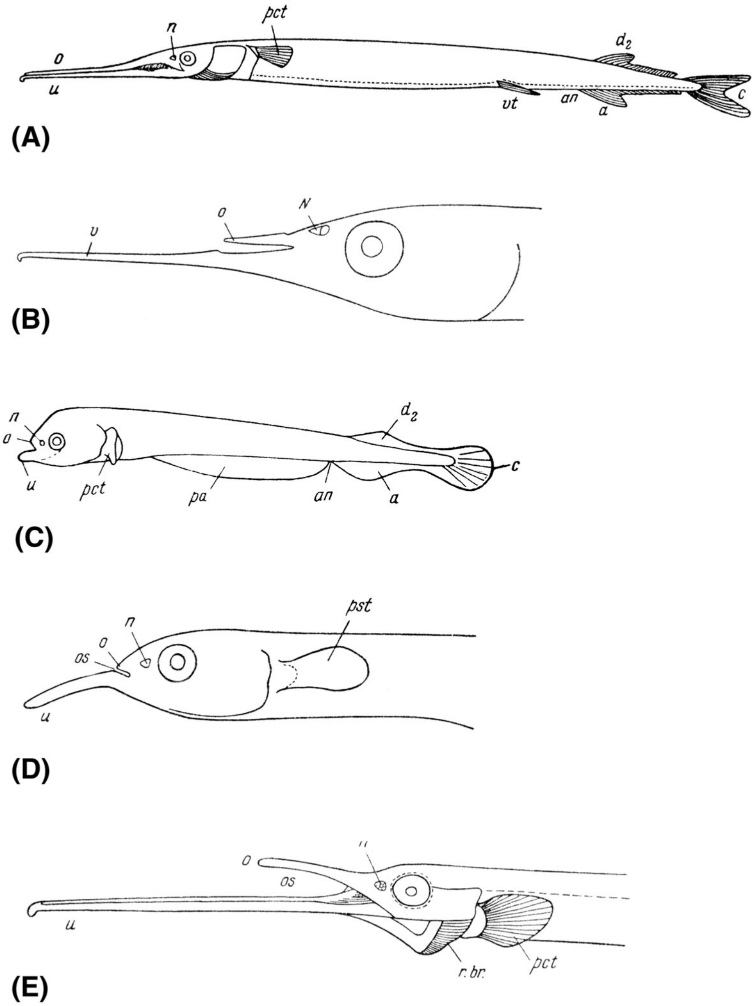

Fig. 2 The development of *Belone acus* as an example of anaboly. **a** Adult *Belone acus*. Lower (*U*) and upper (*O*) jaws are strongly elongated. **b** Head of an adult *Haemiramphus*. The upper jaw (*O*) is much shorter than the lower jaw (*U*). **c** A 10 mm larva of *Belone acus.* **d** A 21 mm larvae of *Belone acus.* **e** A 9,1 cm *Belone acus. a* anal fin; *an* anus; *C* caudal fin; d_2 posterior dorsal fin; *N* nasal pit; *Os* mouth; *p. a.* preanal fin; *pct* pectoral fin; *r. br*. Radii membranae branchiostegiae; *vt* ventral fin. (from Sewertzoff A. N. 1949, 403)

(Fig. 2). This relates to von Baer's law, which claimed 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 maintained that *morphogenesis* was a period lasting from the beginning of ontogeny to the stage at which an individual acquired its most characteristic features. Therefore anaboly could be defined as an extension of morphogenesis. The exact connection between von Baer's law and anaboly consists in the fact that anaboly takes place when the last stages of the morphogenesis of a certain organ, which are similar to the adult organ in the ancestor, were completed by added new stages of ontogenesis (Sewertzoff 1931, 275). Hence, Sewertzoff argued, anaboly is the simplest, the slowest and, phylogenetically, the most basal mode of phylembryogenesis (Sewertzoff 1934).

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

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

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

In summary, the theory of phylembryogenesis distinguished 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. Recapitulation could not therefore be a reliable method for reconstructing phylogenies. At the same time phylembryogenesis—postulating variability at all stages of ontogeny—enabled the integration of the ontogeny-phylogeny problem into the framework of Darwinism. Further work in Russia along these lines, an attempted synthesis between the phylembryogenesis theory, evolutionary morphology and population genetics, was later undertaken mostly by Schmalhausen and his school.

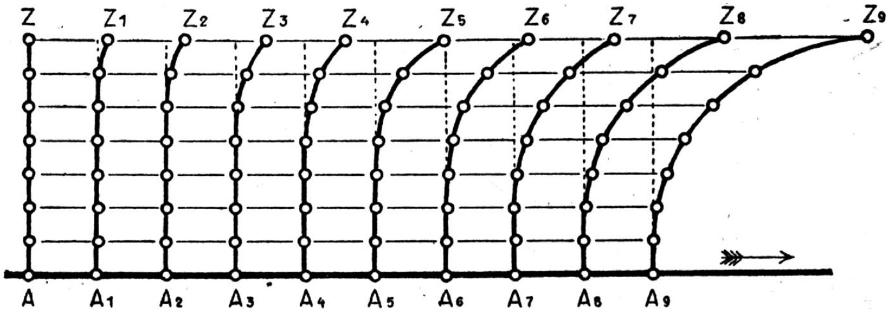

Fig. 3 The law of terminal modification. The *vertical lines* symbolize ontogenetic pathways. *Horizontal heavy lines* manifest the continuity of the development from one egg cell to another. From the typological viewpoint, the ''terminal modifications'' mean the gradual transition of one type into another (from Naef 1917, 57)

3 Adolf Naef and his "law of terminal modifications"

Sewertzoff viewed Adolf Naef's approach to the problem of recapitulation as similar to his own, owing to Naef's "law of terminal modifications" (Naef 1917, 57; Fig. 3). In Sewertzoff's view Naef's ideas were quite close to those of Fritz Müller. Although the same basic assumption that phylogeny is due to modified ontogeny, was shared also by Victor Franz, Walter Garstang (1868–1949), Adam Sedgwick (1854–1913) and Gavin de Beer (Sewertzoff 1949, 389–397), Sewertzoff paid special attention to Naef's version of the relationship between phylogeny and ontogeny.

Naef was one of the crucial figures of idealistic morphology, a current in the biological and paleontological sciences in the second half of the nineteenth century and the early twentieth century, mainly in Germany. The idealistic morphologists called their science "systematic morphology" or "comparative morphology" (Rieppel 2011a, b). Though they used the so-called typological method as the foundation for their research programs, typology was only one element, however 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. He looked for a general doctrine of form, for the *idea* of a certain structure, which escaped pure observation and simplistic explanations. This 'idea' could be expressed in different forms and could be grasped indirectly by means of empirical studies.

In the first decades of the twentieth century, the theoretical landscape was so heavily influenced by typological ideas—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, 2006). However, unlike the early typology, this new movement, explicitly opposed their own typological method to that of evolutionary morphology. Its proponents were 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. 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 shared the same understanding of the basic principles of typology, 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 aimed 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 broad theoretical perspective. His new morphology was to be built on the "sound foundation of old idealistic morphology" (Naef 1919, 13).

Naef, along with other idealistic morphologists, found this "sound foundation" in Goethe's works. 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 should be distinguished, which could 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 whereby this could be achieved was comparative morphology, employed to distinguish general features from particular ones. In this way Naef abstracted, from the diversity of random variations, a network of correlated general characters, which comprised a type (Naef 1923, 390). The type, according to Naef, was a kind of mathematical abstraction, but it could also (actually or potentially) be expressed in a specific organism. The variations around a certain type, which he called the "circle of forms" (*Formenkreis*), can be deduced logically. Naef's method advocated first of all the collection of all knowledge about the type inductively, and then the deduction of all possible forms. The sum total of the "circles of forms" constituted the foundation for a new systematics. Naef labelled his approach the "new synthesis" or "systematic morphology". Its purpose was to order the forms by describing their places in the whole system. Therefore, it was essentially a descriptive science, and Naef thought that its importance for evolutionary theory derived mainly from its descriptive nature, as the best way 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 comparing a range of organic structures. This descriptive procedure was to be made prior 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 were considered similar if they could 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, which is labelled a type. The type can sometimes simultaneously be an abstraction and 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, that 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 to crystals 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:

> 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).

Naef saw the core of Haeckel's research program in the biogenetic law, and hence significantly revised this concept. 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 was more a scientific model without mystical features than a platonic idea. His morphology was a *dynamic* theory of phylogenetic-ontogenetic relations. This dynamism was 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 developed by means of processes that Naef called "morphogenesis". Yet morphogeneses were based on germinal development, which is, again, of a rhythmic-cyclical nature. This dynamic approach allowed Naef to reformulate Haeckel's biogenetic law.

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) the obtainment of 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, 32) and thus Sewertzoff's anaboly. And he explicitly rejected any suggestion of 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). As one might expect, Naef believed that the early stages of ontogenesis, showing a higher degree of generality, are "relatively conservative" and therefore hardly suitable for Sewertzoff's (and Schmalhausen'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 (and Victor Franz's) approach to ontogeny and phylogeny. It was central in Naef's theoretical system and his advocacy of idealistic morphology. The concepts of "type", "typical similarity" (or dissimilarity), together with the "law of terminal modification" were essential instruments for creating a "natural systematic", 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 were 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* essentialistic. 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 maintain a balance between his theoretical assumptions and empirical inquiries. This can be seen, first of all, in his scrupulous work on the morphology and phylogeny of molluscs, especially cephalopods (Naef 1911, 1913). In later periods he worked on vertebrates, especially tetrapods (Naef 1931), and made significant inquiries into their embryology, an activity in which he was motivated by the necessity to prove his law of terminal modifications on a more general basis.

4 Conclusions

Naef and Sewertzoff championed the idea of an evolutionary impact of ontogeny on phylogeny. This was a radical revision of Haeckel's biogenetic law, which claimed that phylogeny was a "mechanical" cause of ontogeny, yet without proposing any concrete mechanism for their supposed reciprocal influence. Sewertzoff's phylembryogenesis and Naef's terminal modifications instead outlined various ways in which ontogeneses could evolve. They can therefore be seen as forerunners of contemporary evo-devo.[1]

Sewertzoff's concept of archallaxis (which was later adopted 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 of a structuralist morphology, his results were not incommensurable with, and were potentially translatable into the language of, Darwinian evolutionary morphology (Reif 1998).

We agree that a debate about the relative evolutionary importance of the early versus late stages of ontogenesis would also be possible between two Darwinians, 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 in his belief that the early stages of ontogenesis were quite conservative. Further outcomes of this conservatism were the epistemological objectives promoted by idealistic morphology. As Naef emphasised, 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 (*nachträglich*) does a typologist elaborate scientific criteria for distinguishing the typical from the atypical (Naef 1931, 95). Reformulated in contemporary terms, Naef's (and Goethe's) "artistic intuition" refers to a preconditioned methodological bias, forcing a researcher to "see" typical features in the ontogeneses in question. In other words, in accordance with the Goethean concept, by morphologically comparing various organic forms, Naef always looked for the typical, whereas Sewertzoff's spiritual eye was free from the necessity of intuitively looking for a norm, or for von Baer's increase of generality in the developmental processes. 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 acted within two different theoretical worlds, but the very dynamism that Naef brought to his concept "corrupted" the essentialist features of his idealistic morphology, and brought him close to the pro-Darwinian evolutionism of Sewertzoff.

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[1] For the definition of evo-devo see e.g. Hall (2000), Gilbert (2003).

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