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BOOK REVIEW

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PHYLOGENETIC SYSTEMATICS: HAECKEL TO HENNIG

Olivier Rieppel

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In this book, Olivier Rieppel has collected several papers written over the last 5 years on different aspects of the (pre-) history of phylogenetic systematics. A certain amount of re-writing has taken place to make the book into a coherent whole, and new chapters have been added (Chapters 4, 8 and 9). Not all of the papers on which the book is based are easily available, so having Rieppel′s writings collected into a book is valuable also in this respect. As the subtitle says, the book starts with chapters on Ernst Haeckel (and Carl Gegenbaur), who for a while both worked at Jena University and infused traditional, idealistic comparative morphology with evolutionary thinking, inspired by Charles Darwin′s "On the Origin of Species." The chapters that follow go through different traditions or schools important in the history of biology in the German-speaking world, including holistic biology, "Aryan" biology and different varieties of idealistic biology. Because historical research on these topics has largely been published in German, only those of us who read German have had access to it. Here, Olivier Rieppel does a valuable service to the scientific community in that he writes in depth about these topics in English. In the last two chapters, the development of phylogenetics, from the Stresemann school in Berlin to Willi Hennig, is described in some detail.

The main message of Rieppel′s book is that Hennig′s work must be understood against the background of a rather peculiar German situation in which idealistic morphology was a strong, if not dominant tradition in biology well into the first half of the 20th century, and for example population genetics was very weak. Rieppel argues convincingly that "Henning′s *magnum opus* of 1950 - *Grundzüge einer Theorie der Phylogenetischen Systematik* (Outlines of a Theory of Phylogenetic Systematics) - [was directed] not so much against competing schools of biosystematics, but rather against German idealistic morphology" (Rieppel p. xiv).

Olivier Rieppel′s book includes "Introduction and Preview" and nine chapters: Chapter 1. The Evolutionary Turn in Comparative Anatomy, Chapter 2. Of Parts and Wholes, Chapter 3. The Turn against Haeckel, Chapter 4. The Rise of Holism in German Biology, Chapter 5. The Rise of German "Aryan Biology," Chapter 6. *Ganzheitsbiologie*, Chapter 7. The Ideological Instrumentalization of Biology, Chapter 8. A new Beginning: From Speciation to Phylogenetics and Chapter 9. *Grundszüge*: The Conceptual Foundation of Phylogenetic Systematics.

The first chapter covers how Gegenbaur and Haeckel tried to synthesise idealistic morphology and Darwin′s theory of evolution. In the second chapter "of Parts and Wholes," Rieppel first gives an overview of the Kantian thinking about laws in nature that was prevalent in German science during the first half of the 18th century, with names such as Karl Ernst von Baer and Matthias Schleiden (the botanist, professor in Jena). He also mentions the cell theory from 1838 and Schleiden′s book *Grundzüge der wissenschaftlichen Botanik* (1842/43). The cell was for Schleiden (and Theodor Schwann) the paradigmatic biological individual.

Most of the second chapter is devoted to an overview of Ernst Haeckel′s most important ideas, and where his inspiration came from. The ideas of Haeckel′s academic teachers, for example Johannes Müller and Alexander Braun in Berlin, and Haeckel′s reaction to these ideas are laid out in detail in "Single cause, complex effect" and "levels and modes of individuality." We particularly liked the part about "changing metaphors of order in nature: the ladder, the tree, and the web," where Rieppel teases apart and describes how Haeckel and others managed to go from a static "scala naturae" to a dynamic conception of evolutionary relationships between organisms.

It is now more than 150 years ago when Ernst Haeckel (1834–1919) published his first major scientific work, "Generelle Morphologie der Organismen," in 1866. Here, he for the first time started to formulate his "Biogenetisches Grundgesetz" (Biogenetic law), which he later developed further in a monograph on calcareous sponges ("Die Kalkschwämme") in 1872 (Haeckel 1872). Neither "Generelle Morphologie" nor "Die Kalkschwämme" were ever translated into other languages and reached a limited audience even in the German-speaking lands. In his "General Morphology," he also 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 introduces a system of the existing groups of organisms based on genealogy rather than the old typological and idealistic ideas (Hoßfeld, 2010; Hoßfeld, Levit,

& Olsson, 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 of his “General Morphology” can be seen also as a first attempt to establish evolutionary morphology and evolutionary embryology as new fields of research (Olsson, Levit, & Hoßfeld, 2010). In the seventh chapter, Haeckel also formulates his ideas for a biological anthropology based on Darwin′s theory of evolution (Hoßfeld, 2016).

Haeckel choose the tree as a model for the depiction of natural relationships between organisms (Hoßfeld & Levit, 2016; Hoßfeld, Watts, & Levit, 2017; Rieppel, 2011). The root symbolises a common primordial form or ancestor, from which all other forms emerge. Haeckel writes that the “natural systems of organisms is their natural genealogical tree,” that is based on palaeontological, embryological and systematic data, the so-called “threefold parallelism” that was so important to Haeckel′s thinking. In the “General Morphology,” he published eight phylogenetic trees and divided all living organisms into three kingdoms—animals, plants and protists. He thought that evolution affected everything from inorganic matter to man and believed in the unity of body and soul, and the unity of spirit and matter. This monism guided Haeckel′s work from the “General Morphology” to his last book on “Crystal souls” in 1917. 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 F. Meckel 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, 1866; II: 300). He later coined the terms *Cenogenie* (secondary adaptation) and *Palingenie* (true recapitulation) (Haeckel, 1874).

It is sometimes said that Ernst Haeckel failed to build a school of devoted pupils, not least because many turned against him when he went from doing empirical science to mostly propagating his monist philosophy. It is therefore pleasing to read the last part of chapter 2 “Reaching out beyond Jena,” where Rieppel shows how several Haeckel students spread the gospel from Jena—each in his own way—across Europe. Rieppel touches upon for example the polish botanist Strasburger (of textbook fame in Germany), Fritz Müller (1821–1897), Oscar Hertwig (1849–1922) and the Swiss scientist Arnold Lang (1855–1914), who all studied under Haeckel in Jena and went on to develop distinctive careers in biology.

In chapter 3, “The turn against Haeckel,” the empire of idealistic biology strikes back against Ernst Haeckel. The main focus is on Antonio Abel (1875–1946) and Adolf Naef (1883–1949), based on Rieppel′s earlier papers (Rieppel, 2012a,b). Especially, the extensive description of Naef′s ideas and world view are impressive. This is probably the best exposition of Naef′s complicated and complex ideas available. Naef was one of the crucial figures in idealistic morphology, a current in biology and palaeontology, which in its supreme manifestation could be found in the second half of the nineteenth and the beginning of the 20th century in Germany. The idealistic morphologists themselves called their science systematic morphology or comparative morphology. They used the so-called typological method as 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 & 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 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 palaeontology—that one can talk about a renaissance of idealistic morphology in German biological sciences (Levit & 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, Williams, & Ebach, 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.

Naef′s primary scientific focus was on molluscs and 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"), that is 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, 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. 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. 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. His 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.

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 Alexei N. Sewertzoff's (and Victor Franz'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," that is 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 (Levit, Hoßfeld, & Olsson, 2004, 2015).

In the following ("political") chapters four, five and seven, Rieppel discusses in detail the "Rise of Holism in German Biology" (Rudolf Virchow, Wilhelm Roux, Hans Driesch, Oscar Hertwig), "The Rise of German ('Aryan') Biology" (Wilhelm Troll, Herman Weber, Ernst Lehmann) and "The Ideological Instrumentalization of Biology" (Gerhard Heberer, Walter Zimmermann). With Heberer and Zimmermann (Chapter 7), the author presents two of the central figures of the so-called "Synthetic Theory of Evolution (Evolutionary/Modern Synthesis)." The evolutionary synthesis of the 1930s and 1940s was one of the most successful scientific theories of the twentieth century in biology. With its acceptance, many of the controversies that had shaped the discussions about evolution since Darwin's *Origin of Species* (1859) came to an end. This unification of evolutionary biology was achieved on a Darwinian basis. Together with selection, which was regarded as the only causal factor leading to adaptation, further evolutionary factors were integrated. Mutation and recombination were identified as the sources of genetic variability. The important effects of population size were stressed, in particular for small populations, where chance effects limit the power of selection. In addition, geographic isolation was seen as an important prerequisite for the splitting of a species into two separate species. This synthetic theory of evolution or Synthetic Darwinism has dominated evolutionary biology since the early 1950s (Junker & Hoßfeld, 2002, 2009). When Ernst Mayr visited Europe in May 1954 he noticed in his "Travel Notes": "In Germany — now a clerical state — the anti-evol[utionary] movement is particularly strong […]. Just like McCarthy synonymizes liberalism and communism, thus after the war evolution was synonymized with the most typological selectionism, and biology with Nazi racism." History of biology and in particular the history of Darwinism have been extremely handicapped in Germany by this widespread point of view. Historians interested in scientific ideas were repelled by the prospect of dealing with pseudo-scientific ideological concepts. Social historians on the other hand who published on German biology during the Third Reich were primarily interested in the political context, racial ideas and eugenics. This reinforced the impression that the history of Darwinism in these years was mainly an ideological movement dominated by political interests (Hoßfeld, 2016; Junker & Hoßfeld, 2009). Walter Zimmermann's (1892–1980) influence was nearly completely restricted to Germany. In Germany, however, his book *Vererbung "erworbener Eigenschaften" und Auslese* (*Inheritance of "Acquired Characteristics" and Selection*, 1938) was considered to be one of the central books of the emerging Synthetic Darwinism. Already in his first book (*Phylogenie der Pflanzen*, 1930), Zimmermann argued for gradualism and against special laws and causes of macroevolution. He emphasised that there is no empirical or theoretical necessity to accept macromutations as a mechanism for macroevolution. Small mutations and selection are sufficient to explain all evolutionary phenomena. Irreversibility in evolution, for example, is just a consequence of the improbability that a number of mutations occur exactly in the reversed way. As early as 1930, Zimmermann was convinced that there was enough data from genetics, empirical and theoretical population genetics, biogeography, morphology, palaeontology and systematics to demonstrate that mutation, recombination, selection and isolation are the relevant factors of evolution. He strongly rejected Lamarckian ideas and the notion that there are fundamental differences between micro- and macroevolution. Zimmermann's 1938 book *Vererbung "erworbener Eigenschaften" und Auslese* was a greatly expanded version of his 1930 theory. Particularly important for the evolutionary synthesis in Germany was a collective work: Gerhard Heberer's *Evolution der Organismen* (1943). In 1959, a second expanded edition and 1967 to 1974 a third edition were published. Heberer's *Evolution der Organismen* was the most representative work of Synthetic Darwinism in Germany. It is remarkable that the book is—with few exceptions—without any reference to national socialist ideas. The major exceptions are Heberer's preface, but not his article on macroevolution, and the contributions by the anthropologists Otto Reche (1879–1966) and Hans Weinert (1887–1967). This is true even for the contributions of authors who published in favour of national socialism in other places. One important reason was the scientific character of the book. This explanation is not sufficient, since, for example Zimmermann's book of 1938, which has a comparable scientific claim but contains rather extensive political parts (Hoßfeld, 1997; Reif, Junker, & Hoßfeld, 2000).

In the in-between sixth chapter "Ganzheitsbiologie"—Rieppel focuses on some specific examples, such as bridge-building between anatomy and ecology (Friedrich Alverdes, August Thienemann, Adolf Remane), bringing fossils to life (Otto Jaekel, Othenio Abel, Johannes Weigelt) or discussing *völkisch* spirit in evolutionary biology (Karl Beurlen). One of the central figures during this period was the zoologist and anthropologist Adolf Remane from Kiel. His main biological concerns were morphology and phylogeny but he also worked on ecology, marine biology and various other topics covering virtually all higher groups of animals from marine invertebrates to mammals. Outside the German-speaking countries, he is probably best known for his discovery of the interstitial fauna (1952), the meiofauna within the interstitial spaces in the sand, his research on the biology of brackish water and his theory on the origin of the coelom within the Bilateria which combined the enterocele theory with the origin of metamerism. Remane regarded the coelomic pouches in archimeric organisms such as echinoderms and the gastric pouches of Cnidaria as homologous and thus the Bilateria as derived from Cnidaria-like ancestors. This implies that the stem species of the Bilateria already displayed a coelomate organisation and that the coeloms in all subgroups of the Bilateria, specifically in the two major lineages—Spiralia and Radialia—are homologous. Elegant as Remane's views may be, against the background of modern morphological and systematic research, his theory must be considered refuted. Although Remane worked extensively on the theoretical foundations of systematics and phylogenetics, his findings and theories remained widely unnoticed in the English literature, partly because he mainly published in German (Zachos & Hoßfeld, 2006). An important question concerning Remane is his attitude towards idealistic morphology. Curiously, in his book from 1952, he seems to reject idealistic morphology rather vigorously. He repeatedly stressed that the philosophical core of idealistic morphology was the metaphysical interpretation of results yielded by morphology and by homology research (Remane, 1952, p;. 13f.). The natural system emerging from morphological analyses was then interpreted as revealing the uniform type or *Bauplan*, in other words the idea behind the multitude of similar but different organisms. This type is a metaphysical abstraction and will never be found in nature. Remane on the one hand insists that this does not lower the value of the morphological results themselves (and, indeed, much of the pre-Darwinian knowledge on morphology and systematic relationships is still valid) but on the other hand regrets that there has been no methodological purging in phylogenetics following the introduction of evolutionary thought. His views on idealistic morphology are best depicted by explaining his distinction between what he calls generalised and systematic type. This distinction is basically the same as the one between (idealistic) *Bauplan* and (real) stem species and is outlined in Remane (1948) and in the fourth chapter (*Typus und Stammform*, "Type and stem form") of his 1952 book. Remane explicitly states that idealistic types belong to the realm of natural philosophy but are useless for natural science (1952, p. 146, footnote 1). He distinguishes four different types among which the generalised and the systematic types are the most important. Actually, what Remane calls systematic type is far from being what is normally called an idealistic type, but unfortunately he held on to this term, which may have led to some confusion about his attitude towards idealistic morphology. The generalised type aims at depicting all the traits that are shared by a group of organisms. It is an abstraction of living organisms and as such does not itself represent an actual individual (1952, pp. 151f.) but rather the idea of, say, a mammal stripped of every single trait of a *particular* mammal. The similarity to Platonic idealism is obvious (see Rieppel pp. 92 ff.). Remane rejects this idealism and even makes it responsible for "repeated crises in the realm of the theory of descent" (1948, p. 261), citing for example typostrophism as one of these crises. In contrast to the generalised type, the so-called systematic type is an explicitly phylogenetic term. Its reconstruction implies the reconstruction of the ground pattern of the taxon under study (1952, pp. 152ff.). The systematic type is not idealistic but a real organism, namely the stem species (called *Stammform*, *Urform* or *Urtyp* by Remane), and hence may actually be found in the fossil record (1948, 1952, p. 156). Based on an analysis of the publications cited, we reject the idea that Remane was an adherent of idealistic morphology in the tradition of Goethe or Troll. He should be seen as a true phylogeneticist. Remane was not primarily in summary interested in the study of evolutionary mechanisms because he was committed to the patterns rather than to the processes of evolution. Nevertheless, as his most productive years fell within the time of the Modern Synthesis and he was convinced that the evolutionary process should form the basis of biological systematics, Remane commented extensively on the new view of evolution (Zachos & Hoßfeld, 2006).

In Chapter 8, "A new beginning: from speciation to phylogenetics," Rieppel first deals with the Stresemann school, started by the ornithologist Erwin Stresemann (1889–1972) who had studied under Ernst Haeckel in Jena in 1908. This makes Stresemann one of Haeckel′s last students before Haeckel retired from teaching. Stresemann spent a long career at the Berlin Natural History Museum as Curator of the bird collections and was also a professor at the Humboldt University in Berlin. Prominent members of the "Stresemann school" include Ernst Mayr (1994–2005) and Bernhard Rensch (1900–1990), who both contributed importantly to the "Modern Synthesis" of evolutionary biology. The connection to Willi Hennig and phylogenetic systematics is that one member of the Stresemann school, Wilhelm Meise (1901–2002) became Curator of the Natural History Museum in Dresden in 1929. Originally an ornithologist, Meise was also interested in other flying vertebrates (frogs, lizards, snakes). An 18-year-old high school (Gymnasium) student attracted Meise′s attention. Willi Hennig (1913–1976) did a homework in which he expressed his concern for the decline of systematics. Meise suggested that the young Willi Hennig revise taxonomically the genus *Dendrophis*, a group of "flying" snakes from Australia. Later Hennig was to specialise entirely on entomology, but the early studies were important for his development as a scientist. Rieppel writes (p. 294) "These early studies foreshadow some issues that would figure prominently in Hennig′s later phylogenetic systematics: problems of the species category and issues of speciation, the aspiration to discover lawfulness in variation, the polarization of primitive and derived characteristics in relation to the evolutionary origin of a species or subspecies, and - perhaps most importantly - an all-pervading crossing of specializations."

The last chapter, "Grundzüge: the conceptual foundations of phylogenetic systematics" concentrates on the direct background to and development of Willi Hennig′s classic book from 1950 "*Grundzüge einer Theorie der Phylogenetischen Systematik,*" (Hennig 1950) which was later translated as "*Phylogenetic Systematics*" in 1966. Lost in translation is the emphasis that Hennig put, already in the title, on his work as the foundations of a **theory** of phylogenetic systematics. A very valuable aspect of this chapter is that Rieppel, in his typical manner, devotes a lot of energy and space to explaining the philosophical inspiration behind Hennig′s work. This might not be known to many readers, and again only those who read German can be acquainted with the philosophy of Theodor Ziehen (1862–1950). So which aspects of Ziehen′s philosophy were important for Hennig (and other biologists such as Rensch)? Rieppel writes (p. 307) "…Ziehen rejected an indeterministic world view, and based his epistemology on universal lawfulness that governs not only the physical world (Ziehen′s causal laws) but also the mental world." Hennig also embraced Ziehen′s complicated concept of "order," and thought that pylogenetics can only be a true science when "order" is used to identify useful characters in an objective fashion. This is where Henning introduces his concept of a "character-bearer" or *Semaphoront*. The semaphoront is "the ultimate element of the biological system" defined as "the individual… during a… infinitely small, period of its life" (Hennig, 1966).

Another philosophical underpinning of Henning′s work is that he considered species to be individuals that are born, live and die (go extinct). Rieppel points out that this is in fact an old tradition in German biology and traces it all the way back to the nature romanticism of Schelling. In Hennig′s system, it is actually not the case, as is often assumed, that a species A that splits into two species B and C dies. Henning writes already in 1947 (Rieppel points this out on page 315) that the stem species continues to live in its daughter species (Hennig, 1947).

Rieppel′s book ends with subchapters on the phylogenetic hierarchy, cladograms and the heterobathmy of characters. These are well-known aspects of Hennig′s work, but again Rieppel points to the philosophical inspiration behind Hennig′s ideas. Our last remark is on "heterobathmy" of characters. This is a term borrowed from the botanist Armen Takhtajan (Hennig had earlier used the term *Spezialisationskreuzungen*) and refers to the fact that all organisms are made up of a mixture of primitive and derived characters. Hennig drew the conclusion that no group can exist that is either completely primitive or completely derived in all its characters. This fact is a necessary precondition for the reconstruction of sister-group relationships and thus for the creation of phylogenies in the first place. In the end, as comprehensive as Rieppel′s book is, maybe the most illuminating parts is where he shows the development of the ideas that ultimately end up influencing Hennig′s work. We are not aware of any book that is as strong on this point as Rieppel′s *Phylogenetic Systematics: Haeckel to Hennig*.

A last remark about writing style. The writing is often quite dense, but this also means that the reader can learn a lot on each page. Readers not well versed in philosophical terminology might find it rough going in some places, as terms are often just stated rather than explained. The historical context of political and societal development in Germany in the 19th and first half of the 20th century is hardly described at all, and readers might want to read about this in parallel.

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