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The Road from Haeckel: The Jena Tradition in Evolutionary Morphology and the Origins of "Evo-Devo"

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Abstract. With Carl Gegenbaur and Ernst Haeckel, inspired by Darwin and the cell theory, comparative anatomy and embryology became established and flourished in Jena. This tradition was continued and developed further with new ideas and methods devised by some of Haeckel's students. This first period of innovative work in evolutionary morphology was followed by periods of crisis and even a disintegration of the discipline in the early twentieth century. This stagnation was caused by a lack of interest among morphologists in Mendelian genetics, and uncertainty about the mechanisms of evolution. Idealistic morphology was still influental in Germany, which prevented a full appreciation of the importance of Darwin's theory of natural selection for comparative morphology. Evolutionary morphology and embryology failed to contribute significantly to the modern synthesis of evolutionary biology, thereby probably delaying the integration of developmental biology into modern evolutionary biology. However, Haeckel's student Oscar Hertwig, as well as Victor Franz and Alexej N. Sewertzoff from a younger generation, all tried to forge their own synthetic approaches in which (inspired by Haeckel's work) embryology played an important role. Important for all three researchers were attempts to refine, and sometimes redefine, the biogenetic law, and to find new scientific explanations for it (and for the many exceptions to it). Their research was later more or less forgotten, and had little influence on the architects of the modern synthesis. As the relationship between evolutionary and developmental biology is now again rising in importance in the form of "Evo-Devo", we would like to draw attention to how this earlier research tradition grappled with similar questions to those now on the agenda, albeit from sometimes quite different perspectives.

Key words: biogenetic law, embryology, Evo-Devo, Victor Franz, Oscar Hertwig, Ernst Haeckel, morphology, Nikolai A. Sewertzoff

1. Introduction

In his introduction to the first volume of *Handbuch der vergleichenden und experimentellen Entwickelungsgeschichte der Wirbeltiere*,[1] published in 1901, Oscar Hertwig described two important traditions in the history of evolutionary research (*Entwicklungslehre*) in the nineteenth century. The older was the morphological tradition, which was later succeeded by the physiological tradition after Theodor Schwann and Matthias Jacob Schleiden had founded cell theory. This latter tradition was dominant when Hertwig was writing his introduction.

The rapid success of the older morphological school at the beginning of the nineteenth century depended to a large degree on the use of the comparative method. Anatomists and zoologists had realized that their sciences needed to go beyond the description of single natural objects to make comparative studies of living organisms and their organ systems in order to be able to formulate general laws of morphogenesis (O. Hertwig 1901: 35). Descriptions of embryos of different animals and comparisons with both the adults and with embryos of other species became common. This descriptive method was often tied to philosophical discourse (e.g. the speculative *Naturphilosophie* of Lorenz Oken, F. W. J. Schelling and others). This early research in comparative embryology was very successful and many important fundamental discoveries were made in the first half of the 19th century by K. E. von Baer, E. Huschke, H. Rathke, F. Keibel, and F. Meckel, among others (Goebbel and Schultka 2002).

Through the dual input of the cell theory and Darwin's theory of evolution, the goal and purpose of this type of research was formulated afresh, and a new field of research was opened up in which comparative anatomy was united with embryology, using the new research tools (such as better microscopy techniques) which had become available (Allen 1981). The cell theory proved to be especially useful in investigations into vertebrate development undertaken by Robert Remak ("*Untersuchungen über die Entwicklung der Wirbeltiere*",[2] (1850–1855) and others. Here the role of different germ layers for organogenesis was discussed in the context of detailed investigations into the origins of specific tissues. The importance of Darwin's ideas was great: "With Darwinism the speculation in the area of evolutionary history has received new impulses, less through Darwin himself than through Haeckel" (O. Hertwig 1901: 52).[3] Haeckel was a strong proponent of integrating Darwin's ideas into the existing research traditions in comparative anatomy and morphology, and was an efficient propagandist as well; his ideas became very widespead.

In this paper, we point out the importance of the tradition that emanates from Haeckel for keeping research into ontogeny and phylogeny integrated in the institutional context of research performed at the University of Jena (Di Gregorio 1995). Our starting point is Haeckel's discussion of the "threefold parallelism" in evolutionary biology, and we use three individuals as exemplars of how these ideas were developed further: Haeckel's student Oscar Hertwig and two of Haeckel's scientific "grand-students", Victor Franz and Alexej N. Sewertzoff. Our main focus is on the relationship that these researchers had to the ideas encapsulated in the "biogenetic law", how they developed Haeckel's ideas further, and yet also criticized them. It will also become clear that the establishment of evolutionary morphology in Jena through Haeckel and Gegenbaur acted as an important stimulus to the development of embryology *sensu lato* in Germany and beyond (Gegenbaur 1859; Dullemejer 1980; Ghiselin 1980; Nyhart 1987, 1995; Riedl 1983).

2. Haeckel's ideas on phylogeny and ontogeny

Following the publication of Darwin's (1859) *On the Origin of Species*, it became important to interpret existing research domains in the light of Darwin's ideas which were applied from early on to the question of the connection between ontogeny and phylogeny (Haider 1953; Gould 1977). Haeckel used comparative anatomy and embryology as ways to prove the theory of descent with modification. Like F. Meckel and his school, Haeckel also 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. Haeckel used the term "*Entwicklung*" (development) for both the development of the individual and "development" over evolutionary time. To these two parallels he added a third, based on palaeontological data. In the threefold parallelism of the phyletic (palaeontological), biontic (individual), and systematic developments, he saw one of the greatest, most wonderful, and important phenomena in organic nature (Haeckel 1866, II: 371ff). The explanation of this "threefold genealogical parallel" he called "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*:[4]

> 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).[5]

At the same time Haeckel realized the problems associated with this subject (Ulrich 1968; Uschmann 1966). The "complete and faithful recapitulation" becomes "effaced and shortened",[6] because the "ontogenesis always chooses the straighter road". In addition the recapitulation becomes "counterfeited and changed through secondary adaptations"[7] and is therefore "better the more similar the conditions of existence were, under which the Bion and its ancestors have developed" (Haeckel 1866, II: 300).

In order to describe these problems Haeckel invented the concepts *Cenogenie* (secondary adaptation leading to non-recapitulation) and *Palingenie* ("real" recapitulation) in 1875. He viewed inheritance and adaptation as the driving factors of the evolutionary process. Haeckel also wrote in *Natürliche Schöpfungsgeschichte*,[8] which was published in 1868, that this relationship (the causal nexus between biotic and phyletic development) is the most important and irrefutable proof of the theory of descent with modification. This parallel was first discussed at length as the "biogenetic law" in 1872 in Haeckel's *Monographie der Kalkschwämme*, but the most comprehensive use of the biogenetic law can be found in Haeckel's writings on the *Gastraea*-theory. According to Haeckel, the Gastraea is a hypothetical "Urform" from which all metazoans have evolved. It has left no palaeontological traces and can therefore only be seen as the gastrula stage in the development of many 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).[9]

With his Gastraea-theory, Haeckel thought 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). Although Haeckel's far-reaching generalizations were not generally accepted, embryology soon counted as an indispensible tool for recognizing otherwise uncertain homologies. Although Haeckel's name is closely associated with the term "biogenetic law", the regularities expressed by it were already well known to numerous researchers before Haeckel (Junker and Hoßfeld 2001).

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" from 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, transgress, 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.

The discussions surrounding the biogenetic law exemplify the fertile interaction between embryology and comparative anatomy in the nineteenth century. 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 (see below). These discussions became important milestones in the history of evolutionary developmental biology. In sharp contrast and competition with evolutionary embryology, Wilhelm His developed a reductionist embryology in the 1870s. His was uninterested in using embryology to understand phylogeny, and worked instead on the direct, mechanical influences on the development of organic forms. The formation of the embryo should ideally be explained by the deformations of an elastic sheet (His 1874). This was the beginning of the "*Entwicklungsmechanik*" tradition most famously associated with Wilhelm Roux (Mocek 1974, 1998).

Since the end of the 1990s, there has been renewed interest in the disputes between Haeckel and his adversaries (Richardson et al. 1997, 1998; Bender 1998; Hoßfeld 1999). Like many times before, the main subject of criticism was Haeckel's plates comparing embryos of different taxa, published in his books *Natürliche Schöpfungsgeschichte* (1868) and *Anthropogenie oder Entwickelungsgeschichte des Menschen*,[10] (1874), where he used them to explain the biogenetic law. Haeckel made these drawings to illustrate his ideas, and they are not drawn directly from observations of embryos, but idealised for pedagogical clarity. The fact that real embryos do not actually look like Haeckel's drawings (for the forgery debate, see Braß 1906, 1909; Dacqué 1904; Jüngst 1910; Mandel 1883; Schmidt 1902, 1909; Teudt 1909) was often not the biggest problem, although many resarchers in Haeckel's time pointed it out. Instead, Haeckel's inference that animals had a common origin was the really important matter. It was, for instance, criticised by His. Haeckel had such a firm belief in the theory of descent that he used it to hypothetically deduce what embryos from species of which he had no material "had to" look like. For example, almost no human embryos were at his disposal. Haeckel made hypothetical deductions from the material at hand, thereby filling the gaps in the history of descent. We think that his adversaries did not attack the biogenetic law as such as much as they used it as a means to an end. What they really attacked was Darwinism and its dissemination by Haeckel.[11]

3. Two generations of German developmental biologists and morphologists

3.1. *Oscar Hertwig (1849–1922) – one of Haeckel's students*

Haeckel's student *Oscar Hertwig* was one of leading biologists of the late nineteenth and early twentieth centuries. His reputation is built upon his broad interests (general biology, experimental and descriptive embryology, sensory and marine biology, systematics, comparative anatomy, cell biology) as well as his many scientific discoveries.

Oscar Hertwig studied medicine in Jena together with his brother Richard from 1868. There they came under the influence of their teachers Carl Gegenbaur and Ernst Haeckel. Haeckel inspired them to join him in morphological research. In the summer of 1869, the Hertwig brothers studied at Zürich University, but then returned to Jena and made their first scientific investigations on ascidian development in Haeckel's Zoology Institute. After a short stint in the war against France, the brothers were back in Jena for the winter semester of 1870/71. They then both spent the summer semester in Max Schultze's laboratory in Bonn, and learnt the techniques of microscopy. They also finished their doctoral theses in Bonn, and both became doctors of medicine in 1872. Oscar's thesis was on "The development and structure of the elastic tissues in the ear". The brothers then became Assistants in Schultze's department. Oscar soon returned to Jena and decided to do his *Habilitation* there. During a trip in March/April 1875 to the Mediterranean (Villefrance-de-Mer), he made a great discovery – he observed the fertilization of the sea urchin egg. This became the central tenet of his *Habilitationsschrift*, which he finished later the same year. The Hertwig brothers spent time together in Messina (1876/77), and then both became so called "*außerordentliche*" professors in Jena in 1878. In 1881 Oscar was given the chair in Bonn, succeding his teacher Gustav Schwalbe. Both brothers were elected to the Leopoldina academy in 1881.

During his time in Jena, Oscar Hertwig published his first book. The topic was tooth development in amphibians and its importance for the development of the skeleton around the oral cavity.[12] He conducted further studies on fertilization in nematode worms, amphibians, and a variety of marine invertebrates, as well as studies on the comparative anatomy of the dermal skeleton of fishes. With his brother, and using the techniques of microscopy which he had learned form Schultze, he also started to study the development of the germ layers in cnidarians. This led to important results regarding the role of the germ layers in organogenesis.[13] Having included chaetognaths in the germ layer studies in the spring of 1879, the brothers described that the coelom forms via an outpocketing from the archenteron.[14] Building upon Haeckel's "Gastraea-Theorie" (1874), the Hertwig brothers then suggested, in their "Coelomtheorie" (1881), that the development of all germ layers can be explained by the simple principle of epithelium folding. The coelom theory led to investigations of mesoderm development, and Oscar became convinced that vertebrates are enterocoelous, the mesoderm being formed from the blastopore border by cells which slide in between endoderm and ectoderm. In addition, Oscar also continued the experimental studies on sea urchins, again collaborating with his brother. The focus was now on hybridization and on the influence of chemical and physical (such as gravity) factors on fertilization and cell division.[15]

A crucial theoretical contribution while Oscar Hertwig was in Jena was his "Kernideoplasma" theory from 1884. According to this theory, the carrier of inheritance is the nucleus. Similar ideas were put forward by other researchers at this time (e.g. C. Naegeli's "ideoplasma" and W. Fleming's "Chromatin") and contributed to a lively discussion about inheritance. Then, in 1886, Oscar Hertwig published the first edition of a textbook on the comparative embryology of vertebrates, *Lehrbuch der Entwicklungsgeschichte des Menschen und der Wirbeltiere* (1886b),[16] which was to appear in ten editions by 1915. In 1900 a short version was published, *Die Elemente der Entwicklungslehre des Menschen und der Wirbeltiere*, aimed at students and physicians. This textbook was translated into many languages and became perhaps the leading textbook on embryology in its time.

After seven years as Professor in Jena, Oscar was offered the chair in comparative anatomy in Berlin in 1887. In 1888 he took up the position and became part of a faculty with some of the most distinguished researchers of the day, such as A. von Bardeleben, E. du Bois-Reymond, R. Koch, R. Virchow, and W. Waldeyer. Construction of a new institute, "Anatomie II", began in 1890, and was completed two years later. In 1897 the name was changed to "*Anatomisch-biologisches Institut*" to better reflect Hertwig's area of activity. Oscar was very successful in Berlin: he became a member of the Prussian Academy of Sciences in 1893 and was awarded the Helmholtz Medal in 1917, among other honors. In 1904/05 he was the Rektor of Berlin

University and in 1913 one of the founders of the Kaiser Wilhelm Institute for Biology in Berlin-Dahlem. He retired on April 1, 1921. Since 1960 the "Anatomisch-biologisches Institut" has been called the "Oskar Hertwig House" (Wagner 2001).

Oscar Hertwig's scientific work in Berlin concentrated to a large degree on gametogenesis in the nematode *Ascaris*. He discovered the meiosis during spermatogenesis, which made it clear that eggs and sperm are produced in the same way with respect to the number of chromosomes (they were both haploid).[17] He also published on frog development and malformations,[18] and developed the view that all cells in the embryo receive the same hereditary material[19] (in opposition to the views of A. Weismann and W. Roux, who attributed the differences between cell types to different subsets of "determinants"). He called his theory of development "*Biogenesis-Theorie*" – in opposition to Weismann's germ plasm theory (Churchill 1970). These ideas were later developed further by O. Mangold and H. Spemann.

Oscar Hertwig's relationship with his old teacher Ernst Haeckel deteriorated after 1900, when Hertwig had developed his criticism of "Darwinism" – here meaning selectionist explanations – and in particular its application to ethical, political, and social questions (Weindling 1991).[20] Hertwig also criticised the biogenetic law, something Haeckel saw as a defection (*Abfall*) from Darwinism (Uschmann 1959: 101). Especially in the book *Das Werden der Organismen* [The becoming of organisms] from 1916, Hertwig argued that the undirected variation which Darwin assumes and documents is not enough to explain the changes and progress seen in the evolutionary history of organisms. Drawing on the ideas of Lamarck and Naegeli, Hertwig tried to develop his Biogenesis theory into an explanation of the (in his view) directional, regular and progressive evolutionay changes as brought about partly by external and partly by internal causes. Hertwig rejected applying the concept "struggle for existence" to human affairs, and in 1922 published a book, *The state as organism*, in which he saw the human states or nations as developing biological entities of a higher order, that is, as superorganisms.

Regarding the pre-history of evo-devo, some further books and papers by Oscar Hertwig are of interest:

1. *Ueber die Stellung der vergleichenden Entwickelungslehre zur vergleichenden Anatomie, zur Systematik und Descendenztheorie* (*Das biogenetische Grundgesetz, Palingenese und Cenogenese*) [On the position of comparative embryology to comparative anatomy, systematics and the theory of descendence] from 1906; Handbuch der vergleichenden und experimentellen Entwickelungslehre der Wirbeltiere [Handbook of the comparative and experimental embryology of vertebrates] part 3, chapter X, pp. 149–180.

2. *Das biogenetische Grundgesetz nach dem heutigen Stand der Biologie* [The biogenetic law according to the current standpoint of biology]. *Internationale Wochenschrift für Wissenschaft, Kunst und Technik.* Vol. 2, 1907, pp. 63–70, 91–98.
3. *Das ontogenetische Causalgesetz. Die Elemente der Entwicklungslehre des Menschen und der Wirbeltiere* [The ontogenetic causal law. Basic development of man and vertebrates], 4th edn., 1910, pp. 438–450.
4. *Allgemeine Biologie* [General Biology], 3rd edn., chapter 28 "*Die Biogenesistheorie und das biogenetische Grundgesetz*" [The Biogenesis theory and the biogenetic law], 1909, pp. 666–675.

Oscar Hertwig uses similar arguments in all four texts. For instance, in 1906 he claimed: "Comparative anatomy and comparative development are two sister sciences, which have the most intimate relationship to each other, complements each other reciprocally in their purposes, and have the same goal" (O. Hertwig 1906: 150)[21]. And later in the same book: "It is the task and goal of comparative development and comparative anatomy to establish the regular conditions, which are fundamental for the morphogenesis of plants and animals"[22] (ibid.: 176). Hertwig argued that there are two main reasons why a reform of the Haeckelian biogenetic law is necesssary:

> Firstly it is impossible to characterize scientifically the ontogenetic stages of an organism as a recapitulation of the forms which have followed each other in the long line of ancestors; secondly the external similarities of embryonic forms to lower species of animals do not allow any inference of a common descent, as is so often made (ibid.: 441).[23]

Oscar Hertwig wanted a more rigorous approach to comparative embryology than just assuming that ontogeny can tell us what the phylogeny must have been like. His careful discussions about the role of internal and external factors in evolution are important contributions to a debate that is still ongoing today.

3.2. *Victor Franz (1883–1950) – Haeckel's academic grandson*[24]

Victor Franz was born in 1883 and obtained his high school diploma (*Abitur*) in 1902 and studied natural sciences, in particular zoology, in Breslau (now Wroclaw in Poland) between 1902 and 1905. With Willy Kükenthal as his advisor, he produced a Ph.D. thesis on shark eye anatomy and histology and received his degree in 1905. In 1906, Franz worked for a few months in the Zoology Institute in Halle (Saale), and then moved to the marine biology field station (*Biologische Anstalt*) on the island of Helgoland in the North Sea, where he worked under Friedrich Heincke until 1910. Then he went to Ludwig Edinger's Institute of Neurology in Frankfurt am Main (Hoßfeld

2000a). In November 1913, Franz was hired as editor in the natural science department of the Institute for Bibliography in Leipzig, where Haeckel's son-in-law Hans Meyer was active. Franz served for four years in the army in the western front during WWI, and was then offered the Ritter professorship in Phylogeny in Jena. Franz was to remain in Jena for the rest of his life, and enjoyed a successful time in research and teaching. He had more then thirty graduate students and wrote more than two hundred papers and books. Franz became an "*außerordentlicher*" professor in 1924 and was given the chair in "Phylogenetic zoology, heredity and history of zoology" in 1936.[25] In addition, he was Director of the Ernst Haeckel House between 1935 and 1945. Franz was an active Nazi before and during WWII, and was consequently dismissed from his professorship on September 13, 1945 (Hoßfeld 2000b). He died in Jena in 1950.

Franz had a very broad education in histology as well as morphology and physiology (under the tutelage of Arnold Lang and Willy Kükenthal), which enabled him to do interdisciplinary work in evolutionary biology. He had originally belonged to the camp (the so-called "*Vervollkommnungsnegierer*") which denied that evolution is progressive, producing ever more perfect organisms (Franz 1907a, 1907b). From 1910 onward, however, he changed his mind and tried to give the concept "*Vervollkommnung*" (improvement) some scientific content. He thereby placed himself in a tradition that includes, for example, Johann W. von Goethe, Haeckel, Karl Ernst von Baer, Ludwig Plate, and Paul Kammerer (Franz 1911a: 364, 1911b, 1920a: V, 1937; Haeckel 1866: 370, 550). Largely building upon Haeckel's ideas, Franz formulated a concept of "improvement" in 1911, and in 1920 a "law of the superiority of differentiation and centralisation."[26] In 1927, he postulated his four "biometabolic modi" (see below). Between 1920 and 1935, he published a number of papers of importance for the theoretical understanding of the connection between embryology, morphology and evolution (Franz 1920b, 1927, 1935, 1951).

Franz saw his own contribution to the development of the theory of evolution foremost in his concept of "improvement" (Franz 1943: 220),[27] but he also worked on the biogenetic law. By creating his "biometabolic modi", which builds upon the work of von Baer, Fritz Müller and Haeckel, Franz tried to give a genetic and developmental explanation of the biogenetic law (Rehkämpfer 1997: 177–182). Thereby he intended not so much to contribute to the old conflict between morphology and physiology (Starck 1965: 62), but to use such "modi" to accomplish a new and exact formulation of the biogenetic law (Uschmann 1953; Peters 1980; Trienes 1989). He divided the evolutionary changes of ontogeny into:

1. Transgression, extension or prolongation of the ontogeny beyond the former adult stage [. . .][28]
2. Shortening or abbreviation of the ontogeny in comparison to the former adult stage [. . .],[29]
3. Divergence or deviation of the ontogeny in comparison to the corresponding former adult stage. The deviation occurs in two forms, as far as we can see: a) larger with each stage [. . .], b) only at a certain stage [. . .]
4. A change in ontogeny that culminates at a certain stage" (Franz 1927: 39).[30]

Franz realized that the biogenetic law, even when augmented by Haeckel's cenogenesis concept, did not suffice as an explanation and replaced it with his four "metabolic modi": 1. Prolongation, 2. abbrevation, 3. ontogenetically increasing 4. ontogenetically culminating deviation of the ontogeny" (Franz 1927: 39).

An empirical example used by Franz to establish the causality between organisation and "improvement" was the accommodation of the vertebrate eye, which according to him improves as we go "up" from "lower" to "higher" vertebrates (Franz 1934). The best overview of Franz's ideas, which are otherwise scattered in numerous papers, is his book *Der biologische Fortschritt – Theorie der organismengeschichtlichen Vervollkommnung* [Biological progress – The theory of improvement during the history of organisms] from 1935. In just 82 pages it gives a summary of his work up until then. Franz first explains his central concepts, such as centralisation, differentiation and "degree of superiority",[31] and then goes on (with the help of examples) to derive "the energetic theory of organismic improvement".[32]

4. A Russian import – Alexej N. Sewertzoff (1866–1936)

Aleksej N. Sewertzoff was born in 1866 in Moscow. His father was the zoologist Nikolaj A. Sewertzoff. He started to study natural sciences, in particular zoology, at Moscow University in 1885. Sewertzoff was a student of Michail A. Menzbir, Ivan M. Sechenov, Karl von Kupffer and Kliment A. Timiryazev. In 1895 he defended his Masters thesis *O razvitii zatylochnoy oblasti nizshikh pozvonochnykh v svyaz, s voprosom o metamerii golovy* [On the development of the neck in lower vertebrates in connection to the metamerism of the head]. He then spent three years doing research at marine biology field stations (Banyuls, Villefranche, Naples) and in zoology laboratories (Munich, Kiel). Sewertzoff finished his Ph.D. thesis *Metameria golov elektricheskogo skata* [Head metamerism in the electric ray] in 1898. Thereafter he worked as "Extraordinarius" professor of Zoology in Dorpat (now

Tartu in Estonia) between 1898 and 1902, and held the chair in Zoology in Kiev from 1902 until 1911. In 1911 Sewertzoff was called to the chair in Zoology at Moscow University, where he founded a research institute for Evolutionary Morphology in 1930. Sewertzoff died on December 19, 1936 in Moscow, and the institute was renamed after him (The Sewertzoff Institute for Evolutionary Morphology and Palaeozoology of the Academy of Sciences of the Soviet Union). Sewertzoff is seen as the doyen of an important school of evolutionary morphology in the Soviet Union, and was a member of both the Soviet Union and the Ukraine academies of science (Hoßfeld 2001).

In 1931 Sewertzoff published an important book in German, *Morphologische Gesetzmäßigkeiten der Evolution* [The morphological regularities of evolution]. Here he summarized the results which he and his many students and collaborators had collected since 1891 on the comparative anatomy of vertebrates.[33] Results from investigations into the morphology, embryology and palaeontology of vertebrates were brought together in Sewertzoff's discussions, something he called the "old method of threefold parallelism" and attributed to Haeckel (Sewertzoff 1931: 8). In the famous lecture which Haeckel held in Stettin in 1863 at the thirty-eighth meeting of the "society of German scientists and physicians", entitled *Über die Entwicklungstheorie Darwins* [On Darwin's theory of evolution], he talks for the first time about the

> [. . .] threefold parallelism between the embryological, systematic, and palaeontological development of organisms, this threefold step-ladder, which I think is one of the strongest proofs of the truth of the theory of evolution (Haeckel 1863: 29).[34]

As the main goal of his book Sewertzoff writes that he:

> [. . .] gave [him]self the task [. . .] to, based on the existing factual material from comparative morphology, come closer to a solution to the problem of the morphological regularities of evolution, and to bring a certain amount of order into the incredible diversity of approaches in phylogenetic research (Sewertzoff 1931: VII, IX).[35]

The book is 371 pages long and divided into two parts. The first part is called "The evolution of lower vertebrates", and consists in a solid exposition of the comparative anatomy of "lower" vertebrates, and provides the basis for the more general evolutionary interpretations. In the section on *Acrania primitiva*, for example, Sewertzoff describes the anatomy of the acraniates, but also uses these data to construct a phylogeny of the "Protocraniata". He also theorizes about the evolution of the Entobranchiata, Ektobranchiata, and *Osteichthyes primitivi*, as well as about the monophyly of vertebrates.

In the second part, "The regularities of phylogenesis", Sewertzoff uses the "morphological regularities" as "the necessary condition for a causal investigation of phylogenesis", which could bring a certain order into "our ideas on the course of evolution" (Sewertzoff 1931: X). Here was a "wide field of activity which researchers have hardly set foot on, and where lots that is new and interesting can be found" (1931: X) by morphologists interested in phylogeny. Sewertzoff distinguished between four different directions which evolution can take:

1. *Aromorphosis* – changes towards an increased level of general vitality.
2. *Ideoadaptation* – no increased level of general vitality, but evolving animals are better adapted to certain environmental conditions than their ancestors were.
3. *Coenogenesis* – embryonic or larval characters, which develop during ontogeny but later disappear. The characters are of direct use to the developing organism while they are expressed.
4. *Physiological-morphological degradation* – reduction of active organs combined with a strong development of the protective and reproductive organs (Sewertzoff 1931: 147–163).

Although interesting in their own right, Sewertzoff's ideas on the different directions which morphological evolution can take are not as important as his notion of a "Theory of Phylembryogenesis". Sewertzoff writes:

> [. . .] that the embryogenesis cannot be explained through phylogenesis alone, but that changes during embryonic development can become reasons for changes in the phylogenesis, and that an exactly coordinated test of phylogenesis and ontogenesis in highly specialized evolutionary lines (Sewertzoff 1931: 263).[36]

is necessary for understanding the "morphological regularities of evolution" (Starck 1965: 60–61). Starting from the idea "that the changes in the structure of the adult animal (phylogenesis on the Haeckelian sense) are dependent upon changes in the process of ontogenesis of these structures themselves,"[37] Sewertzoff distinguished the following modes of phylogenetic change when evolution is "progressive":

1. *Anaboly* (or terminal addition) – the only mode which creates evolutionary changes in accord with the recapitulation "laws" of von Baer, Müller and Haeckel.
2. *Deviation* (deviation in the direction of embryogenesis) – no extension of morphogenesis, only recapitulation of the stages up unitil the deviation.
3. *Archallaxis* – changes to the early stages of embryogenesis. Produces innovations (Sewertzoff 1931: 266–299).

Here Sewertzoff[38] relates his ideas directly to the work of Victor Franz (1924, 1927) on the four "biometabolic modi".

5. Epilogue

What is the relevance of the work of Haeckel and his school for us today? The aims of contemporary "Evolutionary Developmental Biology", according to a recent summary (Hall 2000; as cited in Robert et al. 2001), are to understand: (1) The origin and evolution of embryonic development, (2) How modification of developmental processes lead to the production of new features, (3) The adaptive plasticity of development in life-history evolution, (4) How ecology impacts on development to modulate evolutionary change, and (5) The developmental basis of homology and homoplasy.

If we look at the Gastraea theory of Haeckel, it has been elaborated upon in later attempts at explaining the origin and early evolution of multicellular animals and their life cycles, thereby addressing points 1, 2, 4 and also 5 above. The Gastraea theory has been developed further by researchers interested in the comparative embryology of invertebrates. Some clearly state that their work is based on Haeckel's Gastraea theory, for example Gösta Jägersten. His book *Evolution of the Metazoan Life Cycle* from 1972 is the culmination of his efforts to understand metazoan phylogenesis through studies of the development of marine invertebrates. Jägersten puts forward a general and – in his view – comprehensive theory according to which the original metazoan life-cycle is pelago-benthic and there are later shifts to other types of life-cycles. The earliest metazoans are thought to correspond to Haeckel's Blastaea, which transforms into the Gastraea. Here Jägersten theorizes that when the adult lives benthically, it acquires bilateral symmetry and becomes a "Bilaterogastraea". He also thinks that adult characters have become "pressed down" into the larval phase. Stephen J. Gould, in his classic *Ontogeny and Phylogeny*, describes this as a kind of "acceleration" in his terminology (Gould 1977). This tradition of "speculative phylogeny" (Gould 1977: 233) lives on and maybe the most interesting recent addition has been the Trochaea theory of Claus Nielsen (Nielsen and Nørrevang 1985; Nielsen 2001). Nielsen derives hypothetical ancestors for protostomes and deuterostomes (or Gastroneuralia and Notoneuralia in his terminology) through an elaborate scenario which starts with Haeckel's Blastaea and Gastraea. Haeckel's goal of using the Gastraea theory to show that all metazoans have a common origin has now been reached by other means. Both molecular systematics and morphological investigations reach this result. Ernst Haeckel also thought that embryology was a guide to establishing homologies. Today it is not uncommon to use the expression of regulatory genes – as visualized by *in-situ* hybridization of their mRNA, to suggest that the body parts expressing the same gene or genes in different organisms are homologous. The same problems that were discussed in Haeckel's time now resurface again. Similarity of form or gene expression can have several causes, and common descent is only one of them.

Oscar Hertwig's discussion of internal and external causes of evolution corresponds to the modern debate about the role of developmental constraints in evolution. At one end of the spectrum we have the ultra-selectionists who deny any role for internal or "structuralist" factors in directing evolution. Selection can accomplish anything and there are no constraints. Function determines form. Oscar Hertwig would have been unhappy with this approach; he did not think that selection was a powerful factor in evolution. The current proponents of "developmental constraints" as important for the direction and tempo of evolutionary change might be interested in taking a look at Oscar Hertwig's careful analyses of this difficult issue. Hertwig also criticized the idea that similarities between embryos of different organisms, and even more between embryos of one species and adults of another, can be used as a reliable guide to phylogenetic reconstruction. He was well aware that resemblences can have many causes, including what we would now call convergent evolution. In todays "evo-devo" discussion this would involve points 2, 3 and 4 above on modifications of development, plasticity and "eco-devo".

Franz and Sewertzoff both contributed to the field we now call heterochrony with their suggestions about how to divide up and name the different processes underlying heterechronic change. Victor Franz was grappling with issues that are still causing terminological confusion today. His division into prolongation, abbrevation, and two types of deviation have heuristic value, as has Sewertzoff's division into anaboly, deviation and archallaxis. However, several rounds of debates over the proper terminology for heterochronic processes and mechanisms have come and gone since then and there now exists a confusing number of schemes among heterochrony workers. Understanding the developmental basis of heterochrony remains a challenge, and some progress has been made in identifying "heterochrony genes" in for example the nematode *C. elegans*. Franz was convinced that evolution is progressive. This idea has remained controversial and has been heavily critized. There are several problem with it. First of course what do we mean with "progress" in evolution? Franz thought that selection would automatically lead to more and more well-adapted organisms. He seems not to have thougth that the environment would change so fast as to give rise to a "Red Queen" situation where organisms may not become "improved" despite being selected.

The strength of Sewertzoff's model of evolution lies in bringing together results from comparative anatomy with the new insights into the mechanisms of evolution that were emerging as the "modern synthesis" of evolution (Starck 1965: 60, 1977). It was typical for his school to use data from species between which the phylogenetic relationships were relatively clear to try to answer questions about the underlying evolutionary mechanisms. The tradition to which Sewertzoff belongs, often called evolutionary morphology, had relatively little success in Germany until the middle of the 20th century (Reif, Junker and Hoßfeld 2000). One reason was that many anatomists (e.g. Eduard Jacobshagen, Wilhelm Lubosch, Adolf Naef) made a return to a "pure" idealistic morphology, while others like Franz Weidenreich and Alfred Benninghoff saw the correlation of form and function as the causal explanation of structural evolution. It was not until the 1950s that Sewertzoffian ideas were recycled in Germany, in the interdisciplinary research of Dietrich Starck (who had studied under Franz) and his students (Starck 1978).

Now that the relationship between evolution and development is again becoming a central theme in modern biology, we can see that some of the central issues have deep roots. Using the tools of molecular genetics, researchers are again approaching classical questions in evolutionary morphology, such as head segmentation in arthropods and vertebrates ("*Das Kopfproblem*"), the fin-limb transition, and questions concerning homology (Hall 1998). The origin of evolutionary innovations, and what role developmental changes play, is again a hot topic (Müller and Wagner, in press). This is partly the same issue as the role of caenogenesis and palingenesis in evolution which was very much in the minds of Haeckel and researchers in the tradition emanating from him. There has been a tendency recently to focus on the conservation of developmental processes and mechanisms over large evolutionary timespans – the conserved HOX genes for example – to the detriment of research on how the differences in morphogenesis and adult structure between organisms have evolved. The availability of probes from the fruit fly for genes with effects on early events in development, such as axis formation, which often *are* very conserved, made it easy to look for these genes and their roles in other organisms. We can now see this changing, with studies like Lowe and Wray's (1997) documenting the differences in expression patterns of regulatory genes between organisms.

We hope that the new era of "Evo-Devo" will lead us to a deeper understanding of the mechanisms behind the evolutionary innovations which have led to new structures and functions over evolutionary time. Haeckel, O. Hertwig, Franz and Sewertzoff were all fascinated by the different types of changes which can take place in ontogenetic processes during evolution, but they could often do little more than describe and name these phenomena – for example the different ways in which the biogenetic "law" could be "broken". The phenomena that they described are still with us, however, and it is an important task for contemporary evolutionary developmental biology to discover the underlying mechanisms.

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Notes

[1] In English: "Handbook of the comparative and experimental development of vertebrates."
[2] In English: "Investigations into the development of vertebrates".
[3] German original: "*Mit dem Darwinismus hat die Spekulation auf dem Gebiete der Entwickelungsgeschichte wieder neue Impulse erhalten, weniger durch Darwin selbst als durch Haeckel*."
[4] In English: "General Morphology of Organisms."
[5] German original: "41. *Die Ontogenesis ist die kurze und schnelle Recapitulation der Phylogenesis, bedingt durch die physiologischen Functionen der Vererbung (Fortpflanzung) und Anpassung (Ernährung). 42. Das organische Individuum . . . wiederholt während des raschen und kurzen Laufes seiner individuellen Entwickelung die wichtigsten von denjenigen Formveränderungen, welche seine Voreltern während des langsamen und langen Laufes ihrer paläontologischen Entwickelung nach den Gesetzen der Vererbung und Anpassung durchlaufen haben*."
[6] German original: "*verwischt und abgekürzt*".
[7] German oiginal: "*gefälscht und abgeändert durch secundäre Anpassung*".
[8] In English: "Natural History of Creation."
[9] German original: "*Aus dieser Identität der Gastrula bei Repräsentanten der verschiedensten Thierstämme, von den Spongien bis zu den Vertebraten, schliesse ich nach dem biogenetischen Grundgesetze auf eine gemeinsame Descendenz der animalen Phylen von einer einzigen unbekannten Stammform, welche im Wesentlichen der Gastrula gleichgebildet war: Gastraea*."
[10] In English: "Antropogeny or the evolutionary history of Man".
[11] Compare e.g. the struggles between the Monistenbund and the conservative Keplerbund.
[12] Über das Zahnsystem der Amphibien und seine Bedeutung für die Genese des Skelets der Mundhöhle (1874).
[13] Publications on germ layer development in cnidarians: *Ueber das Nervensystem und die Sinnesorgane der Medusen* (1877/78), *Ueber die Muskulatur der Coelenteraten* (1879), *Die Actinien anatomisch und histologisch mit besonderer Berücksichtigung des Nervenmuskelsystems untersucht* (1880a).
[14] *Die Chaetognathen, ihre Anatomie, Systematik und Entwicklungsgeschichte* (1880b).
[15] *Welchen Einfluß übt die Schwerkraft auf die Theilung der Zellen*? (1885), *Experimentelle Untersuchungen über die Bedingungen der Bastardbefruchtung* (1886a), *Experimentelle Studien am tierischen Ei vor, während und nach der Befruchtung* (1890a).
[16] In English: "Textbook of human and vertebrate development."
[17] *Vergleich der Ei- und Samenbildung bei Nematoden. Eine Grundlage für celluläre Streifragen* (1890b).
[18] *Urmund und Spina bifida. Eine vergleichend morphologische, teratologische Studie an mißgebildeten Froscheiern* (1892).
[19] *Experimentelle Untersuchungen über die ersten Theilungen des Froscheies und ihre Beziehungen zur Organbildung des Embryo* (1893).

[20] *Das Werden der Organismen. Eine Widerlegung von Darwins Zufallstheorie durch das Gesetz der Entwicklung* (1916), *Zur Abwehr des ethischen, des sozialen, des politischen Darwinismus* (1918).

[21] German original: "*Vergleichende Anatomie und vergleichende Entwickelungsgeschichte sind zwei Schwesterwissenschaften, welche in den innigsten Beziehungen zu einander stehen, in ihren Aufgaben sich gegenseitig ergänzen und dem gleichen Ziel zustreben*."

[22] German original: "*Aufgabe und Ziel der vergleichenden Entwickelungsgeschichte und der vergleichenden Anatomie ist die Feststellung der gesetzmäßigen Verhältnisse, die der pflanzlichen und tierischen Formbildung zu Grunde liegen*."

[23] German original: "*Erstens ist es unmöglich, die ontogenetischen Stadien eines Lebewesens als Wiederholung der Formen, welche sich in der langen Vorfahrensreihe einander gefolgt sind, wissenschaftlich zu charakterisieren; zweitens läßt sich aus der äußeren Aehnlichkeit embryonaler Formen mit niederen Tierarten kein Schluß auf eine gemeinsame Abstammung beider ziehen, wie es so vielfach geschieht*."

[24] For more on Victor Franz see Hoßfeld (2000b), Krauße and Hoßfeld (1999) or Penzlin (1994); *Thüringisches Hauptstaatsarchiv* Weimar, *Personalakte Franz*; *Universitätsarchiv* Jena, *Personalakte Franz*; *Nachlaß Franz* in the archives of the Ernst-Haeckel-House, Best. Z.

[25] *Universitätsarchiv* Jena, Best. BA, Nr. 975, p. 211.

[26] German original: "*Gesetz von der Überlegenheit der Differenzierung und Zentralisation*".

[27] Franz uses the words "*Vervollkomnung*" and "*Höherentwicklung*" which in German have subtly different meanings. We have translated both as "improvement".

[28] German original: "*Hinausschreiten, Verlängerung oder Prolongation der Ontogense über das vormalige adulte Stadium* [...]."

[29] German original: "*Abkürzung oder Abbreviation der Ontogenese gegenüber dem vormaligen adulten Stadium* [...]."

[30] German original: "*Abweichung oder Deviation der Ontognese gegenüber ihren entsprechenden vormaligen Stadien. Die Deviation tritt, soweit wir es bisher überblicken, in zweierlei Art auf: a) je Stadium zunehmend* [...], b) *auf ein bestimmtes Stadium* [...] 4. *auf bestimmten Stadium kulminierende Deviation (Änderung) der Ontogenese*."

[31] German original: "*Überlegenheitsgrad*".

[32] German original: "*Ableitung der energetischen Theorie der organismischen Vervollkommnung*".

[33] There are 133 publications until 1931.

[34] German original: "[...] *dreifache Parallele zwischen der embryologischen, der systematischen und der palaeontologischen Entwicklung der Organisme, auf diese dreifache parallele Stufenfolge, die ich für einen der stärksten Beweise der Wahrheit der Entwickelungstheorie halte*."

[35] German original: "[...] *stellte ich mir die Aufgabe* [...] *auf Grund des zur Zeit vorliegenden, vergleichend-morphologischen Tatsachenmaterials dem Problem der Erforschung der morphologischen Gesetzmäßigkeiten der Evolution näher zu kommen und in die ungeheure Mannigfaltigkeit der phylogenetischen Vorgänge eine gewisse Ordnung zu bringen*."

[36] German original: "[...] *daß nicht die Embryogenese allein durch die Phylogenese erklärt werden kann, sondern das Veränderungen während der Embryonalentwicklung Anlaß zu Abänderungen in der Stammesgeschichte werden können und daß eine exakte koordinierte Prüfung von Phylogenese und Ontogenese in engen Spezialisationsreihen*."

[37] German original: "[...] *daß die Veränderungen der Struktur der erwachsenen Tiere (Phylogenese im Haeckelschen Sinne) durch Veränderungen des Ganges der Ontogenese derselben bedingt worden sind*."

[38] Sewertzoff had worked on the testing of the biogenetic law already in 1912 in his *Studien zur Evolutionstheorie.* In this early work his argumentation still follows that of Müller and Haeckel (Sewertzoff 1912).

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