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THE 150TH ANNIVERSARY OF ERNST HAECKEL'S «BIOGENETIC LAW»

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150 ЛЕТ «БИОГЕНЕТИЧЕСКОМУ ЗАКОНУ» ЭРНСТА ГЕККЕЛЯ

150 years ago, in 1866, the Jena zoologist Ernst Haeckel published a book in two volumes and almost 1000 pages long called «Generelle Morphologie der Organismen». Here he formulated for the first time his so-called biogenetic law, famously stating that ontogeny recapitulates phylogeny, which he later elaborated in his 1872 book on calcareous sponges. Here we describe Haeckel´s original idea and follow its development in the thinking of a few of the scientists whose work was inspired by Haeckel. In these book, Haeckel mentioned first time the term «ecology».
Keywords: *ontogeny, phylogeny, biogenetic law, Ernst Haeckel, ecology.*

150 лет назад, в 1866 г., зоолог из Йены (Германия) Эрнст Геккель (1834–1919) опубликовал книгу объемом в тысячу страниц в двух томах под названием «Общая морфология организмов». В этой книге он впервые сформулировал свой знаменитый биогенетический закон, постулировавший, что онтогенез рекапитулирует филогенез. Этот закон он развил в 1872 г. в книге, посвященной известковым губкам. Статья описывает оригинальную концепцию Геккеля и на нескольких примерах показывает, как биогенетический закон повлиял на других ученых. В этой же книге Геккель впервые употребил термин «экология».
Ключевые слова: *онтогенез, филогенез, биогенетический закон, Эрнст Геккель, экология.*

Introduction

It is now 150 year ago that the German zoologist Ernst Haeckel (1834–1919) published his first major scientific work, «Generelle Morphologie der Organismen», in 1866. Here he for the first time formulated his famous «Biogenetisches Grundgesetz» (Biogenetic law), which he later developed further in a monograph on calcareous sponges («Die Kalkschwämme») in 1872. Neither «Generelle Morphologie» nor «Die Kalkschwämme» were ever translated into other langauges, and reached a limited audience even in the German-speaking lands. The popularisation of Haeckels ideas followed in 1868 when a collection of lectures that he had held at Jena University (where he was the first professor of zoology) were published as «Natürliche Schöpfungsgeschichte» («Natural History of Creation»). This popular science book became a bestseller and was also translated into different languages. Here he coined severalnew concepts, and some of themare still in use, such as ecology, phylogeny, ontogeny, and phylum. In this book Haeckel presented his initial ideas on the relationship between ontogeny and phylogeny (biogenetic law) and introduces a system of the existing groups of organisms based on genealogy rather than the old typological ideas [17, 19]. His «oecology» was interpreted as a by-product of the revolution in biology he began in 1866 to make it into a Darwinian science based on causal-mechanical methodology. «Oecology» was for him a branch of physiology replacing the tasks and subject matter of a discipline known at that time as economy of nature. Insofar Haeckel successfully re-introduced the research programme of former *Naturgeschichte* into the post-Darwinian science. Haeckel developed the notion of «Oecology» in his later works, especially in his *Plankton-Studies* of 1890, which is often seen as his most instructive analysis of ecological issues. In fact, however, the genuine objective of the concept of «Oecology» in *Studies* was to reform marine biology by introducing a new systematics based on the principles of *Naturgeschichte.* Yet, the modern term of ecology outlived Haeckel's conceptual framework and emancipated itself from neo-Lamarckian and metaphysical context. Contemporary systematic-integrative ecology developed itself relatively independently from Haeckel's initial use of the term [5, 24, 33, 41, 42]. Compare Haeckel's original explanation of ecology with its modern use [41:140–141]: «By ecology, we mean the whole science of the relations of the organism to the environment including, in the broad sense, all the 'conditions of existence.' These are partly organic, partly inorganic in nature; both, as we have shown, are of the greatest significance for the form of organisms, for they force them to become adapted. Among the inorganic conditions of existence to which every organism must adapt itself belong, first of all, the physical and chemical properties of its habitat, the climate (light, warmth, atmospheric conditions of humidity and electricity), the inorganic nutrients, nature of the water and of the soil, etc.

As organic conditions of existence we consider the entire relations of the organism to all other organisms with which it comes into contact, and of which most contribute either to its advantage or its harm. Each organism has among the other organisms its friends and its enemies, those which favor its existence and those which harm it. The organisms which serve as organic foodstuff for others or which live upon them as parasites also belong in this category of organic conditions of existence. In our discussion of the theory of selection we have shown what enormous importance all these relations have for the entire formation of organisms, and specially how the organic conditions of existence exert a much more profound transforming action on organisms than do the inorganic. The extraordinary significance of these relations does not correspond in the least to their scientific treatment, however. So far physiology, to which this [science] belongs, has, in the most one sided fashion, almost exclusively investigated the conserving functions of organisms (preservation of the individual and the species, nutrition, and reproduction), and among the functions of relationship [investigated] merely those which are produced by the Contributions relations of single parts of the organism to each other and to the whole. On the other hand, physiology has largely neglected the relations of the organism to the environment, the place each organism takes in the household of nature, in the economy of all nature, and has abandoned the gathering of the relevant facts to an uncritical 'natural history', without making an attempt to explain them mechanistically».

How did Ernst Haeckel get the idea to write a very large monograph at this relatively early stage in his career? Clearly he wanted to revolutionize biology by using Charles

Darwin´s recently published evolutionary theory (or theories) as the foundation for this science. He had also secured a professorship and could start to lay out a long-term research program (as we would say today). The immediate reason for sitting down to write this massive work was — at least in part — personal or even private. The historian of biology Robert J. Richards has argued, in «The tragic sense of life», his biography of Haeckel [39], that the effort that went into producing this enormous work, a book of almost 1000 pages published in two volumes, was connected with his reaction to the death of his first wife, Anna Sethe, from puerperal fever shortly after having delivered a daughter. On the day Richards interprets as the most important in Haeckel's life, February 16, 1864, he turned 30, received a prize for his scientific work (the Cothenius medal, Leopoldina), and lost his wife. After this, Haeckel went into a frenzy of work, and completed the *Generelle Morphologie* within a year. Although he remarried, and took several lovers, nothing and no one could replace his beloved Anna.

The *Generelle Morphologie der Organismen* consists of a first volume called «the general anatomy of organisms» («Allgemeine Anatomie der Organismen») and a second volume called «general developmental history» («Allgemeine Entwicklungsgeschichte»). The subtitle is General principles of the organic form-science, founded mechanically through the theory of descent as reformed by Charles Darwin («Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformierte Descendenz-Theorie») The first volume was dedicated to Haeckel´s teacher, the anatomist Carl Gegenbaur, and the second volume to the «founders of the theory of descent», Darwin, Goethe and Lamarck. This book is the key to Haeckels later work, its goal being to apply Darwin´s theory to biology in general, but especially to morphology. Haeckel goes through both the animal and the plant kingdoms, concentrating on morphology and phylogeny [27, 31].

Another important aspect of the book is Haeckel´s attempt to establish a promorphology — a general theory of basic forms — in the first volume. The second volume can be seen as a first attempt to establish evolutionary morphology and evolutionary embryology as new fields of research [35, 36]. In the seventh book, Haeckel also formulates his ideas for a biological anthropology based on Darwin´s theory of evolution [19].

Ernst Haeckel choose the tree as a model for the depiction of natural relationships between organisms [21, 22]. The root symbolizes a common primordial form or ancestor, from which all other forms emerge. Haeckel writes that the «natutal systems of organisms is their natural genealogical tree», that is based on paleontological, embryological and systemic data, the so-called «threefold parallelism» that was so important to Ernst Haeckel´s thinking. In the *Generelle Morphologie* he published eight phylogenetic trees and divided all living organisms into three kingdoms — animals, plants and protists [17–19].

Haeckel 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 *Generelle Morphologie* to his last book on «Crystal souls» [11]. Because the *Generelle Morphologie* did not become the success that Haeckel had hoped for, he arranged for his successful Darwin lectures, attended by 200 students in the winter semester of 1867/68 (a third of all students at Jena University at the time) to be stenographed and later published as *Natürliche Schöpfungsgeschichte*

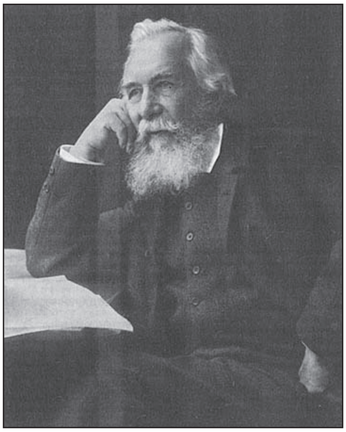

Fig. 1. Ernst Haeckel (Archive of the Ernst-Haeckel-House, Jena)

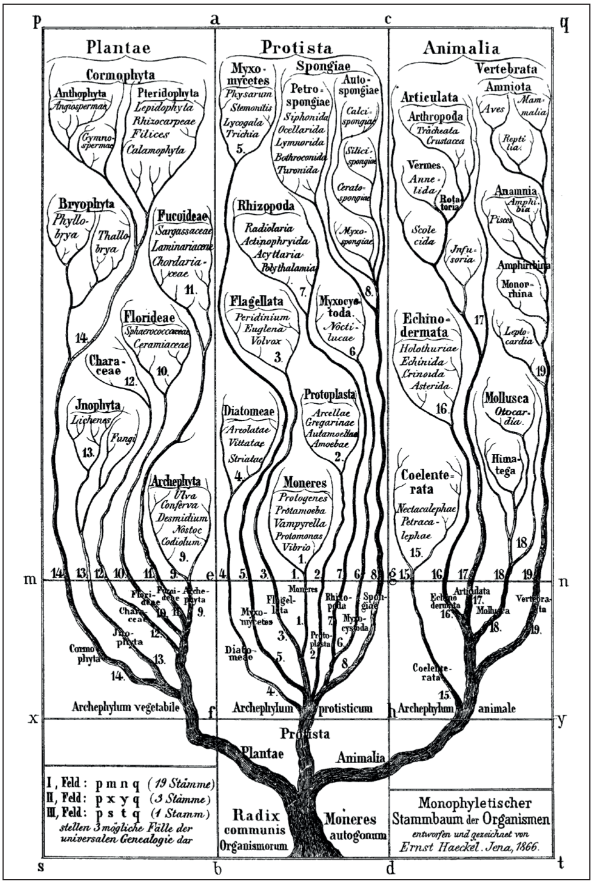

Fig. 2. Tree of Life (General Morphology of Organism, 1866)

in 1868 (translated as «The History of Creation» in 1876). Here he also made some revisions beased on the criticism he had received from Carl Gegenbaur und Thomas H. Huxley. This book was written in a accessible style and, together with the *Anthropogenie oder Entwickelungsgeschichte des Menschen* from 1874 (English translation «Anthropogeny, or the Evolutionary History of Man», became a great succcess. It was translated into many languages and sold extremely well, and made an important contribution to the popularization of the theory of evolution in Europe and beyond [15].

The biogenetic law - more then just embryology?

Having finished the *Generelle Morphologie*, Ernst Haeckel went on a trip to the Canary islands for several months. He did not seem interested in the reactiosn of his colleagues to his, sometimes very polemical, statements in the book. In a letter to Thomas H. Huxley from May 12, 1867 he notes that: «A radical reform of science <…> cannot be undertaken by gently and soft, but only by energetic and reckless means» [26, our translation].

Ernst Haeckel succeeded in showing that anatomy and morphology, as well as developmental biology, could provide important data supporting the theory of descent. Just like J.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

Fig. 3. Ernst Haeckel – Embryo Drawings, Normal Tables (Haeckel, E., 1874. Anthropogenie oder Entwicklungsgeschichte des Menschen. Gemeinverständliche wissenschaftliche Vorträge über die Grundzüge der menschlichen Keimes- und Stammesgeschichte. Leipzig: W. Engelmann)

development, or in short form the 'biogenetic law'». Haeckel wrote about the reciprocal causal relationships in his *Generelle Morphologie der Organismen*:

1. Ontogenesis is the short and fast recapitulation of phylogenesis, controlled through the physiological functions of inheritance (reproduction) and adaptation (nutrition).

2. 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 [7].

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

3. The true and complete repetition of phyletic development by biontic development is reduced and shortened by secondary condensation, since ontogeny strikes out on an ever straighter course. Thus, the longer the sequence of successive juvenile stages, the more true will be the repetition [7: 300].

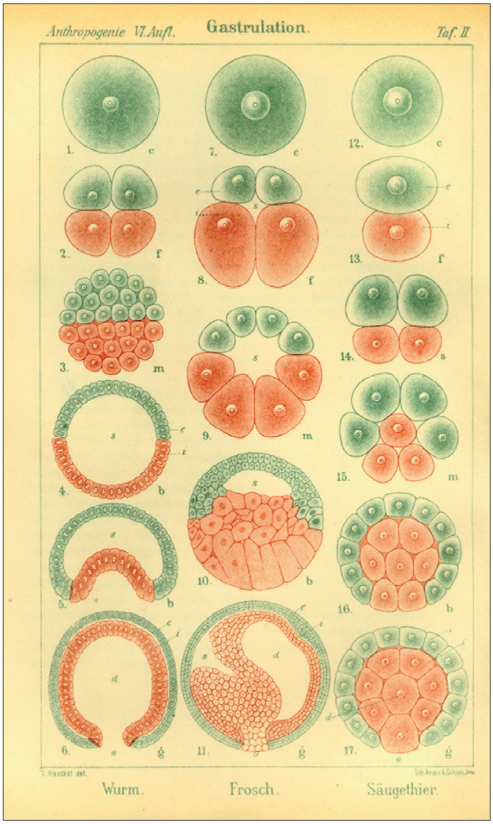

Fig. 4. Gastrulation (Haeckel, E., 1874. Anthropogenie oder Entwicklungsgeschichte des Menschen. Gemeinverständliche wissenschaftliche Vorträge über die Grundzüge der menschlichen Keimes- und Stammesgeschichte. Leipzig: W. Engelmann, Table 2)

In addition Haeckel states:

4. The true and complete repetition of phyletic development by biontic development is falsified and changed by secondary adaptation, since the bion adapts to new conditions during its individual development. Thus, the more alike the conditions of existence under which the bion and its ancestors have developed, the more true will be the repetition [7: 300].

He later coined the terms *Cenogenie* (secondary adaptation) and *Palingenie* (true recapitulation) [6, 10]. Ernst Haeckel developed and applied his biogenetic law further as the «Gastraea theory» in his 1872 book on calcareous sponges.The Gastraea is a hypothetical primordial form («Urform») common to all multicellular animals. Haeckel writes that the Gastraea cannot be found in the fossil record but can be reconstructed from the appearence of a gastrula stage in the embryonic development of most extant animals:

From these identical gastrulae of representatives of the most different animal phyla, from poriferans to vertebrates, I conclude, according to the biogenetic law, that the animal phyla have a common descent from one unique unknown ancestor, which in essence was identical to the gastrula: Gastraea [8: 467].

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 [6, 9, 10].

The theory of evolution and the «Biogenetic Law»

The journalist and plankton researcher Otto Zacharias (1846–1916) was an important popularizer of Haeckel´s «Darwinismus» and corresponded with Haeckel throughout the last quarter of the 19th century [32]. The quotation above illustrates the importance of Haeckel´s so-called biogenetic law for discussions about evolution in this era. In a letter from 1877, Zacharias describes how he came across, at the local marketplace, a pig with «thumbs», which are normally completely absent, developed on both forelimbs. Such atavistic mutations, which bring forth characters that have long been lost in the evolutionary line leading to an extant species, were seen as «throwbacks» to earlier eras, and as important evidence for evolution as descent with modification. So excited was Zacharias by this discovery, that he bought the pig, and after it had been slaughtered and the forelimbs «hacked off», sent at least one of the pigs feet to Charles Darwin and asked for his comments on the phenomenon and its importance for the theory of evolution. Darwin sent the foot to the anatomist W. H. Flower in London and wrote: «The pigs-foot has been dispatched to day per Rail» on May 2, 1877. Flower made a thorough investigation and wrote back to Zacharis that he had seen similar examples before, but this was an unusually well developed «pigs thumb».

Why did atavisms provoke such interest and enthusiasm in those days? An *atavism* is defined as the reappearance in a member of an extant species of a character that has been lost during phylogenesis, such as hind legs in whales or teeth in birds. The direct cause might be that a developmental program that is normally not active in this species has been re-activated. In a classic paper, Brian Hall [12, 13] has reviewed the developmental basis of atavisms. The biogenetic law could take atavisms into account without problems. They were just re-appearences of characters that this species had once possessed during its phylogenesis. That such characters could appear in its present ontogenesis was in accordance with «ontogeny recapitulats phylogeny».

Also Darwin himself pointed out the importance of embryology for revealing community of descent. He put great value on this relationship for systematics [12]. Maybe the most important contribution to discussing Haeckel´s biogenetic law critically was Fritz Müller´s book «Für Darwin» [30]. Müller studied crustaceans and came to the conclusion that evolutionary changes take place mostly through «Abirren» (literally, going astray, here divergence from the original developmental pathway) and «Hinausschreiten» (literally, transgression, here development beyond the endpoint of the original developmental pathway). Thus Müller explained phylogenetic changes by reference to changes in ontogeny, while Haeckel did the opposite — in phylogeny he saw the explanation for ontogeny. The goals were also different. While Müller sought causal explanations, Haeckel erected a law based on his observations and preconceived ideas [1].

The discussions surrounding the biogenetic law exemplify the fertile interaction between embryology and comparative anatomy in the 19th century [14, 15]. They also show that ontogenetic results must be used with caution in evolutionary biology. When the concepts and terminology introduced by Haeckel did not suffice to answer the questions at hand, several biologists tried to supplement or replace the biogenetic law. These discussions became important milestones in the history of evolutionary developmental biology [16, 36, 37].

The Biogenetic law today

Today the concept a a phylotypic stage, a stage where all species belonging to the same phylum are morphologically very similar (like in Haeckel´s embryo drawings), is often replaced by a «phylotypic period» [40]. To illustrate this, the «hourglass model» [29], initially proposed by Duboule [4] and Raff [38], is often used. In this model, the middle part is very narrow, symbolically interpreted as indicating that variation at the midde stages of development is very constrained. Earlier and later stages are more variable. Very early developmental stages can also look very different because of differences in yolk content and thereby egg size, whereas later stages are more variable because the embryo develops more and more of the characters seen in the adult animal. Unlike according to Haeckel´s biogenetic law, similarities between embryos of different species within a phyllum are not considered to be caused by the recapitulation of former adult stages, but the causes a found on the molecular level (transcription factors, signaling pathways etc.).

Today new methods, such as transcriptome analysis [28], are used to test the validity of the hourglass model. It has been shown that animals show similar gene expression patterns at the phylotypic period, when they also look very similar [3, 25]. These molecular mechanisms, which are conserved within a phylum, can explain the morphological similarities (or Bauplan) and function as constraints that limit variation at the phylotypic stage [23].

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