EVOLUTIONARY DEVELOPMENTAL BIOLOGY: ANCIENT ROOTS AND NEW PERSPECTIVES

Lennart Olsson
Friedrich-Schiller-Universität Jena, Erbertstr. 1, D-07743 Jena, Germany

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Contents

Summary

Recently, developmental biology has been infused by evolutionary concepts and perspectives, and a new field of research – evolutionary developmental biology – has been created and is often called EvoDevo for short. However, this is not the first attempt to make a synthesis between these two areas of biology. In contrast, beginning right after the publication of Darwin's "Origin" in 1859, Ernst Haeckel formulated his biogenetic law, famously stating that ontogeny recapitulates phylogeny. Haeckel was in his turn influenced by pre-Darwininan thinkers such as Karl Ernst van Baer, who had noted that earlier developmental stages show similarities not seen in the adults. In this chapter, the history of EvoDevo is first reviewed, especially the tradition emanating from Haeckel and other comparative embryologists and morphologists, which has often been neglected in discussions about the history of EvoDevo and evolutionary biology. This historical part is followed by a short review of the discovery of and importance of Hox genes, the breakthrough that ushered in the new era of synthetic work in EvoDevo. Then an overview is given of some major concepts at the intellectual core of modern EvoDevo, such as modularity, constraints and evolutionary novelties. The relationship between novelty and homology is also breifly explored. The chapter ends with some thoughts on the promise and future of EvoDevo.

1. Introduction

[...] problems concerned with the orderly development of the individual are unrelated to those of the evolution of organisms through time" (Wallace 1986).

The importance of embryonic development for evolutionary biology has been an issue ever since Charles Darwin and Ernst Haeckel. However, Modern Synthesis approaches to evolution have often neglected development or treated it as a black box. Although Wallace's statement cited above is extreme, mid-20th century mainstream evolutionary biology did not feel much need for an integration of developmental biology into its theoretical foundations.

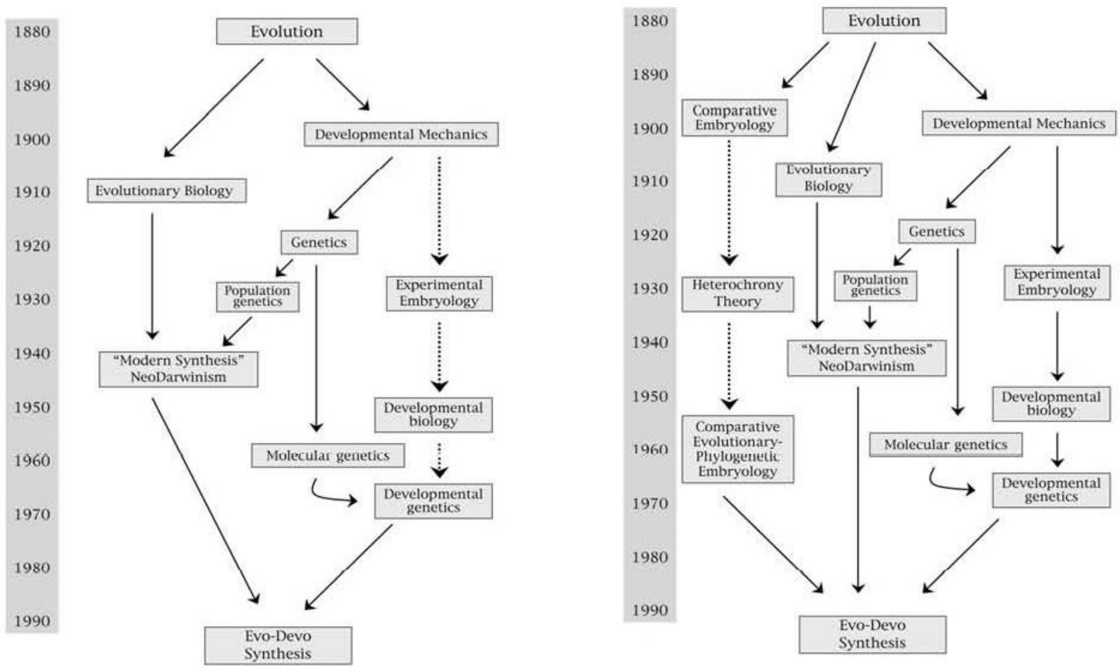

Figure 1. Historical development of the relationship between evolutionary and developmental biology, as depicted in Love and Raff (2003). To the left the "textbook view" that evolutionary biology split up into "Entwickelungsmechanik" and evolutionary biology, followed by a divorce of genetics from experimental embryology - genetics became a research area in its own right. Later the new, molecular genetics fused with developmental biology, resulting in the powerful developmental genetics of the 1980s. Meanwhile, population genetics became the foundation for the Modern Synthesis in evolutionary biology. Currently a new EvoDevo synthesis is underway. To the right is Love and Raff's revised version, where they point out that in addition, there is a line going from the comparative embryology of Haeckel *et al.* over heterochrony research that also feeds into the present EvoDevo synthesis.

The fact that evolutionary questions have been of interest to some developmental biologists between the era of Darwin and Haeckel, i.e. that modern EvoDevo, as the field is often called by its practitioners, in fact has a history, is something that has received little attention. It has even been claimed that "Following a quiescent period of almost a century, present-day evo-devo erupted out of the discovery of the homeobox on the 1980s" (Arthur, 2002, p. 757). In this historical overview I hope to show that the "between Ernst Haeckel and the homeobox" period was anything but quiescent. The recent increased interest in the history of EvoDevo makes it possible to present an overview.

The history of EvoDevo in the Anglo-American world has received renewed attention recently, as exemplified e.g. by the work of Alan Love, whose scheme of the historical development of the relationship between evolution and development is here reproduced as Figure 1. Together with German and Russia colleagues, I have worked on the history of EvoDevo in the German- and Russian-speaking lands. The text in this chapter is based on a recent review (Olsson et al., 2010).

In Love's scheme (Figure 1), he contrasts the "textbook version" (left) with an improved, updated version (right). In the left diagram, evolutionary biology is split from developmental biology, which was dominated by "Entwickelungsmechanik" (Developmental Mechanics) in the first third of the 20th century. The developmental biologist Thomas H. Morgan (1866−1945) is seen as an example of the split between experimental embryology and genetics, which he helped to found and develop into molecular genetics. Another part of genetics, population genetics, became an important part of the Modern Synthesis of evolutionary biology. The progress in molecular biology led to the origin of a developmental genetics which became an increasingly dominant field of developmental biology. In the received view presented to the left in Figure 1, we today see a new EvoDevo synthesis of these two elements, developmental genetics and modern evolutionary biology. It has become clear, however, for example through the work of Love and others on G. R. de Beer (1899−1972) in the English-language tradition, that this is too simple a view. The entire comparative embryology tradition, so strong in the German lands and in Russia in the wake of pioneers like Ernst Haeckel (Figure 2) and Alexander Kowalevsky, is completely left out of the picture. It is important to clarify the role of this tradition, mostly developed by zoologists and at marine biology stations in addition to universities, in the complicated genealogy of today's EvoDevo.

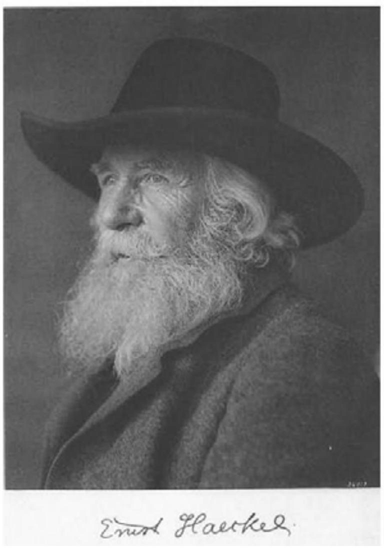

Figure 2. Ernst Haeckel (Bildarchiv, Ernst-Haeckel-Haus, Jena, , with permission).

It is clear that Ernst Haeckel's Gastraea theory has been an inspiration for generations of comparative embryologists in several countries. We have recently investigated how this idea was developed in the 20th century by Scandinavian researchers. The Swedish zoologist Gösta Jägersten (1903-1993, Olsson, 2007) explicitly refers to Haeckel's work and developed a theory of the "Evolution of the Metazoan Life Cycle". This "Bilaterogastraea", a bilaterally symmetrical stage after the Gastraea, builds directly upon Haeckel's ideas. This tradition has been taken up by e.g. Claus Nielsen in his Trochaea-theory from the mid-1980s (Nielsen & Nørrevang 1985).

Victor Franz in Jena und his Russian colleague Aleksej N. Sewertzoff were pioneers of heterochrony research, and also belong to the tradition drawn in the right part of Figure 1, together with heterochrony researchers in the US and Britain, such as Gavin deBeer. Thus, in the last few years a more differentiated view of the history of developmental biology and its relationship with evolutionary theory has started to emerge. This is, however, only a beginning and more work is urgently needed on almost all aspects of this fascinating subject.

2. Fundamental Questions in Evodevo

An important aim of this chapter is to show that the fundamental questions in today's EvoDevo have deep historical roots. Hall (2000) listed them as follows:

1. The origin and evolution of embryonic development
2. How modifications of development and developmental processes lead to the production of novel features.
3. The adaptive plasticity of development in life-history evolution.
4. How ecology impacts on development to modulate evolutionary changes; and
5. The developmental basis of homology and homoplasy.

This also shows that EvoDevo is not restricted to developmental genetics today, but has a broader scope, and as we will see below, this can be explained by its historical roots.

3. History of EvoDevo

"I bought the pig immediately, had it killed and the feet hacked off, and sent them to Darwin" (*German original: "Ich acquirierte das Schwein sofort, ließ dem Niederstechen die Pfoten Abhacken u. schickte dieselben an Darwin"*) Otto Zacharias in a letter to Ernst Haeckel, 21 May,1877.

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

Why did atavisms provoke such interest and enthusiasm in those days? An *atavism* is defined as the reappearance in a member of an extant species of a character that has been lost during phylogenesis, such as e.g. hind legs in whales or teeth in birds. The direct cause might be that a developmental program that is normally not active in this species has been re-activated. In a classic paper, Brian Hall (1984) has reviewed the developmental basis of atavisms. The biogenetic law could take atavisms into account without problems. They were just re-appearances of characters that had once been present during the phylogenesis of this line of descent. That such characters could appear in its present ontogenesis was in accordance with "ontogeny recapitulates phylogeny". Haeckel put great theoretical emphasis on the parallel between the stages of development of the embryo and the series from lower to higher forms of animals studied in comparative anatomy and systematics. Haeckel used the term "Entwickelung" (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).

At the same time Haeckel realized the problems associated with this subject. The "complete and faithful recapitulation" becomes "effaced and shortened", because the "ontogenesis always chooses the straighter road". In addition the recapitulation becomes "counterfeited and changed through secondary adaptations" 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). He viewed inheritance and adaptation as the driving factors of the evolutionary process.

Also Darwin himself pointed out the importance of embryology for revealing community of descent. He put great value on this relationship for systematics. Maybe the most important contribution to discussing Haeckel's biogenetic law critically was Fritz Müller's book "Für Darwin" from 1864. Müller (1864) 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 19th 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 to, and in competition with evolutionary embryology, Wilhelm His developed a reductionist embryology already 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. This was the beginning of the "Entwicklungsmechanik" tradition associated with Wilhelm Roux.

The Importance of Haeckel'S Students For The Development Of Evodevo.

Haeckel's student Oscar Hertwig (1849-1922, Figure 3) was one of the leading biologists in the late 19th and early 20th centuries. He studied medicine in Jena together with his brother Richard from 1868. 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 (*Über das Zahnsystem der Amphibien und seine Bedeutung für die Genese des Skelets der Mundhöhle (1874).).* 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, using the then new microscopy techniques, 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 (*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*)). Having included chaetognaths in the germ layer studies in the spring of 1879, they described that the coelom forms via an outpocketing from the archenteron (*Die Chaetognathen, ihre Anatomie, Systematik und Entwicklungsgeschichte (1880b).).* Building upon Haeckel's "Gastraea Theory", the Hertwig brothers then suggested, in their "Coelomtheorie" (1882) 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 Hertwig 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 (*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).).*

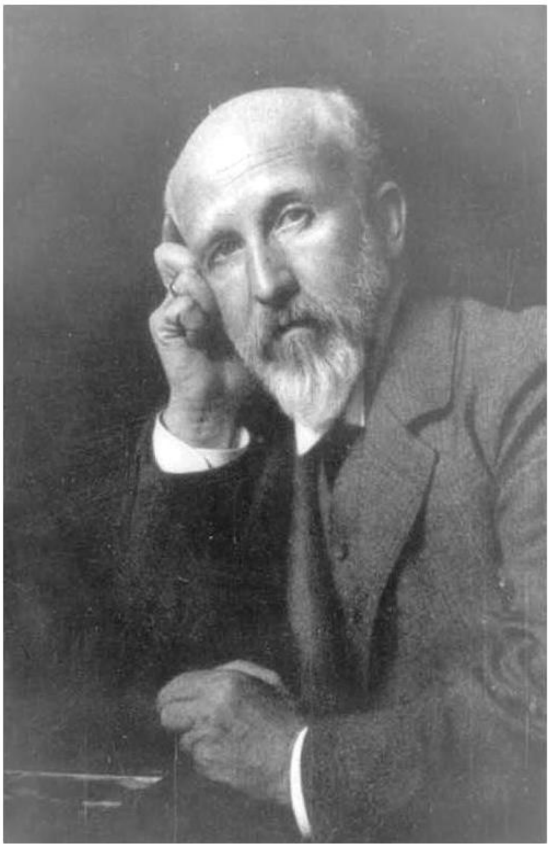

Figure 3. Oscar Hertwig (from Uschmann 1959: 104, with permission).

Oscar Hertwig 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. Oscar Hertwig's scientific work in Berlin concentrated to a large extent 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 as regards the number of chromosomes (they both become haploid) *(Vergleich der Ei- und Samenbildung bei Nematoden. Eine Grundlage für celluläre Streifragen (1890b).)*. He also published on frog development and malformations (*Urmund und Spina bifida. Eine vergleichend morphologische, teratologische Studie an mißgebildeten Froscheiern (1892)),* and developed the view that all cells in the embryo receive the same hereditary material (*Experimentelle Untersuchungen über die ersten Theilungen des Froscheies und ihre Beziehungen zur Organbildung des Embryo (1893).)* (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.

Oscar Hertwig's relationship with his old teacher Ernst Haeckel deteriorated after 1900, when Hertwig had developed his criticism of "Darwinismus" – here meaning selectionist explanations – and in particular its application to ethical, political, and social questions (Weindling 1991). (*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).*) Hertwig also criticized the biogenetic law, something Haeckel saw as a defection ("Abfall") from Darwinism. 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 evolutionary changes as brought about partly by external and partly by internal causes. Oscar Hertwig argued that there are two main reasons why a reform of the Haeckelian biogenetic law is necessary:

> "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).(*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*)

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.

Ernst Haeckel had falling-outs not only with Oscar Hertwig, but with several of his students. In fact, he had a quite negative attitude towards the new histological techniques, and his comparative, phylogenetic approach to development was largely superseded by younger scientists (including his own former students) working in the "Entwickelungsmechanik" tradition founded by Wilhelm His and Wilhelm Roux. So curiously, there is no "Jena School" in the sense of a line of pupils following in the wake of the master, but rather Haeckel attracted many bright students which were to develop their own scientific profiles. In 1908 Haeckel retired from his position as Director of the Institute of Zoology and Jena University offered the position to Ludwig Plate. With the active support of Haeckel himself, Plate accepted the position in January, 1909 and held it until his retirement. Plate developed a synthetic approach that he called "Old-Darwinism", in which he kept the neo-Lamarckian factors that were important also for Darwin and Haeckel, along with orthogenesis and mutationism. Another professor in Jena, Victor Franz (1883-1950), carried the strictly selectionist version of the Haeckelian tradition further. Franz served in WWI and was offered the Ritter professorship in Jena after the end of the war. This was an endowed chair placed in the "Phyletisches Museum", a museum of evolution built by Haeckel and donated to Jena University in 1908, when it celebrated its 350th anniversary. Franz saw his own contribution to the development of the theory of evolution foremost in his concept of "improvement"(*Franz uses the words "Vervollkomnung" and "Höherentwicklung" which in German have subtly different meanings. We have translated both as "improvement")*, 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. He intended to use such "modi" to accomplish a new and exact formulation of the biogenetic law. His ideas on "biometabolic modi" are similar to those of a Russian scientist that visited Jena repeatedly, A.N. Sewertzoff, to which we now turn.

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Biographical Sketch

Lennart Olsson was born in 1961 in Järvsö, Schweden. Born into a country-side family of farmers and workers, where no one had received a college education, he first became a dental technician (1980) and later studied biology, chemistry and history of ideas at Stockholm University, Sweden, obtaining a M.Sc. in Zoology in 1988. Olsson was a graduate student at Uppsala University, Sweden, and finished his Ph.D. in 1993 with a thesis on pigment cell migration and pattern formation in salamanders. He then taught as a Lecturer at Uppsala University and was a postdoctoral fellow with Prof. James Hanken at the University of Colorado, USA, where he started to work on amphibian head development. When still in Uppsala, he started to collaborate on lungfish head development with Prof. Jean Joss in Sydney, Australia. In November 2000, Olsson was tenured as professor of comparative zoology at the Friedrich-Schiller-Universität in Jena, Germany. He has spent sabbaticals at the Konrad-Lorenz-Institute for Evolution and Cognition in Vienna (with Prof. Gerd Müller), at Harvard University (Prof. Hanken), in Sydney (Prof. Joss) and at NESCent (in Durham, USA). Currently, most of the research in his group is focused on the evolution and development of the vertebrate head. Using amphibians and fishes, postdocs and graduate students in Olsson's group study both the developmental mechanisms behind evolutionary novelties and developmental anatomy in a comparative, phylogenetic context. Several studies have investigated the migration and long-term fate of neural crest and somitic cells in embryos and larvae, and the effects of changes in life-history, such as the evolution of direct development and viviparity, on developmental anatomy remain important research themes. Olsson also has an interest in the history and philosophy of biology and works on the history of EvoDevo and comparative morphology in collaboration with Prof. Uwe Hoßfeld (Jena, Germany) and Prof. Georgy S. Levit (Halifax, Canada).