The History of Embryology Seen through the Lens of a Human Embryo Model (Embryo His / Br3) Made by Firma Osterloh in Leipzig

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In our era of computers and computer models the importance of physical models for both research and education in developmental biology is often forgotten or at least underappreciated. One important aspect of embryology is the developmental anatomy of both human and animal embryos. Here we present a particularly valuable model of a human embryo at the end of the fourth week of development (Embryo His / Br3, length – 9,6 mm). The model shows the embryo at 100 times its actual size and was made in the 1930s by Firma Osterloh in Leipzig, Germany. The model can be taken apart to show inner organs such as the heart and the liver, which can also be deconstructed further to show their inner structure. In addition, the developing eye, nose and inner ear can be observed, as well as limb buds and parts of the circulatory system. The fact that the embryo at this stage has a prominent tail and other characters that are later resorbed, could be used to discuss the biogenetic law and other theoretical issues.

Keywords: embryo model, Firma Osterloh, Evo-Devo, embryonic development, developmental physiology, Ernst Haeckel, Fritz Müller, gastraea, didactics in biology.

A short history of embryology and Evo-Devo

The importance of embryonic development for evolutionary biology has been discussed ever since Charles Darwin (1809–1882) and Ernst Haeckel (1834–1919); however, Modern Synthesis (Mayr and Provine 1980) approaches to evolution have often neglected development or treated it as a black box (Mayr and Provine 1980; Olsson and Hoßfeld 2007). The fact that evolutionary questions have been of interest to some developmental biologists between the era of Darwin and Haeckel and modern times, i.e., that Evo-Devo, as the field is often called by its practitioners, in fact has a history, is something that has received little attention (Amundson, 2005; Hall, 2012; Müller, 2008). 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 in the 1980s" (Arthur, 2002, p. 757). But the "between Ernst Haeckel and the homeobox" period was anything but quiescent (Olsson et al., 2009), as is becoming clear through recent work on the history of Evo-Devo. The history of Evo-Devo in the Anglo-American world has received renewed attention recently as exemplified, e.g., by the work of Alan Love (e.g. Love, 2006, 2009; Love, Raff, 2003; Raff, Love 2004; Müller, 2008). We have ourselves concentrated on the history of Evo-Devo in the German- and Russian-speaking lands (Hoßfeld, Olsson 2003; Levit et al. 2004, 2006; Olsson, 2007; Olsson et al. 2006, 2010; Levit, 2007). In Love's scheme (Fig. 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 twentieth 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

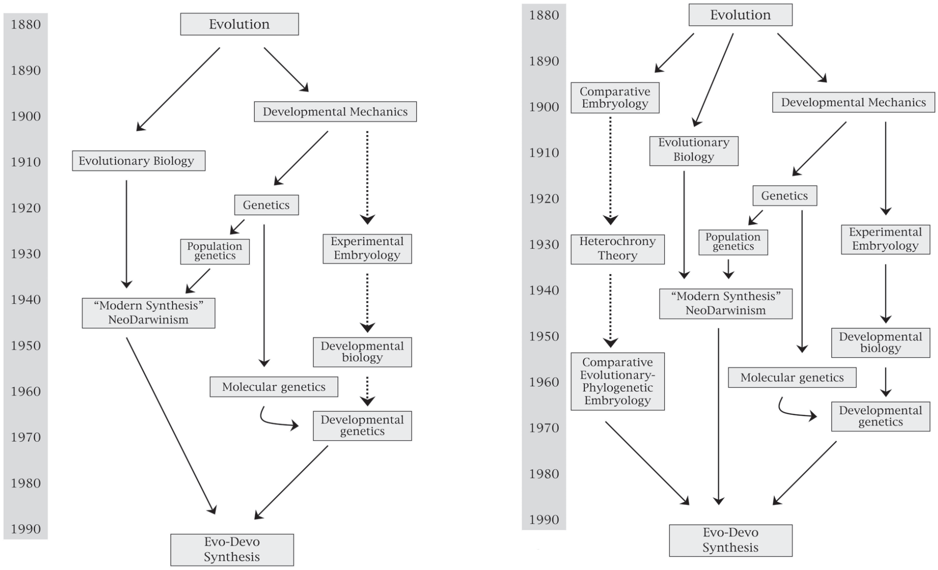

Fig. 1. Historical development of the relationship between evolutionary and developmental biology, as depicted in Love and Raff (2003). To the left the "textbook view" that evoltionary biology split up into "Entwickelungsmechanik" and evolutionary biology, followed by a divorce of genetics from experimental 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 Evo-Devo 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 Evo-Devo synthesis

that later developed into molecular genetics. Another part of genetics, population genetics, became an important part of the Modern Synthesis of evolutionary biology (Junker, 2004; Junker, Hoßfeld, 2009; Mayr, Provine, 1980). The progress in molecular biology led to the creation of a developmental genetics, which became a more and more dominant part of developmental biology. In the commonly held view presented to the left in Fig. 1, we today see a new Evo-Devo 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 [e.g., (Brigandt, 2006) on Gavin 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 and Alexander Kowalevsky (1840–1901; see Raff, Love, 2004), is completely left out of the picture. It is important to clarify the role of this tradition, mostly developed by invertebrate zoologists and at marine biology stations (Naples etc.) in addition to at universities, in the complicated genealogy of today's Evo-Devo. It is clear that Haeckel's Gastraea theory has been an inspiration for generations of comparative embryologists in several countries. The Gastraea is a hypothetical "Urform" from which all metazoans have evolved, according to Haeckel. It has left no paleontological traces and can therefore only be seen as the gastrula stage in the development of many extant animals. Haeckel writes:

> 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, Bd. 1, S. 467).

The zoomorphologist Victor Franz (1883–1950) in Jena and his Russian colleague Aleksej N. Sewertzoff (1866–1936) were pioneers of heterochrony research, together with heterochrony researchers in the US and Britian, such as Gavin de Beer. We have done a bit of research on them and other members of the "Jena tradition" of comparative embryology (Hoßfeld, Olsson, 2003; Olsson, Hoßfeld, 2007; Levit et al., 2004). 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.

Ernst Haeckel, Fritz Müller, and the Biogenetic Law

Ernst Haeckel was inspired by his older colleague in Jena, the anatomist Carl Gegenbaur (1826–1903), who had been instrumental in bringing Haeckel to Jena as a professor. Gegenbaur wrote a number of research monographs and textbooks, which were seen as a model of critical investigation based on an extensive collection of facts, something Haeckel admired. Gegenbaur pioneered investigations into e.g. vertebrate head development in an evolutionary context, and incorporated an evolutionary view in his later work (Hoßfeld et al. 2003). In the pre-history of Evo-Devo, Gegenbaur and Haeckel contributed importantly to creating an evolutionary morphology, specializing on vertebrates and invertebrates, respectively.

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, the "development" of forms as seen in the fossil record. He put great emphasis on this threefold parallelism of the phyletic (palaeontological), biontic (individual), and systematic developments (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* (General Morphology of Organisms):

> 41. Ontogenesis is the short and fast recapitulation of phylogenesis, controlled through the physiological functions of inheritance (reproduction) and adaptation (nutrition).
>
> 42. The organic individual <...> recapitulates through its fast and short individual development the most important 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, Bd. II, S. 300).

Haeckel clearly realized the problems associated with this subject (Ulrich 1968; Uschmann 1953, 1966). 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

Fig. 2. The Osterloh Embryo model, rear view

conditions of existence were, under which the Bion and its ancestors have developed" (Haeckel, 1866, Bd. II, S. 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 what he called "community of descent" (common origin in a phylogenetic sense). He put great value on this relationship for systematics (Darwin, 1871, vol. 1, p. 205). Maybe the most important contribution to discussing Haeckel's biogenetic law critically was Fritz "Desterro" Müller's book *Für Darwin* (Müller, 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, he saw the explanation for ontogeny in phylogeny. The goals were also different. While Müller sought causal explanations, Haeckel erected a law based on his observations, but also on the preconceived ideas encapsulated in the biogenetic law.

In sharp contrast to, and in competition with evolutionary embryology, Wilhelm His (1831–1904) 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 (His, 1874; Brandstetter, 2009). This was the beginning of the "Entwickelungsmechanik" tradition associated with Wilhelm Roux that led to the experimental embryology tradition in the 19th century (Mocek, 1974, 1998).

Teaching Biology, Higher Education, and Embryology

Traditionally, higher education in medical schools and in zoology and botany departments at universities depended on models, wall charts and other pedagogical tools (including microscopes) to convey the complex information about internal and three-dimensional structure that students of medicine and biology need to integrate in their minds in order to achieve mastery of their disciplines. In particular, the embryonic development of humans and other animals poses severe challenges to student's abilities of spatial representation, and therefore embryo models have been, and partly still are, important teaching tools to help students imagine e.g. the complex turns and twists involved in the development of inner organs such as the heart or the alimentary tract and its associated glands. We found a remarkable model of a human embryo at

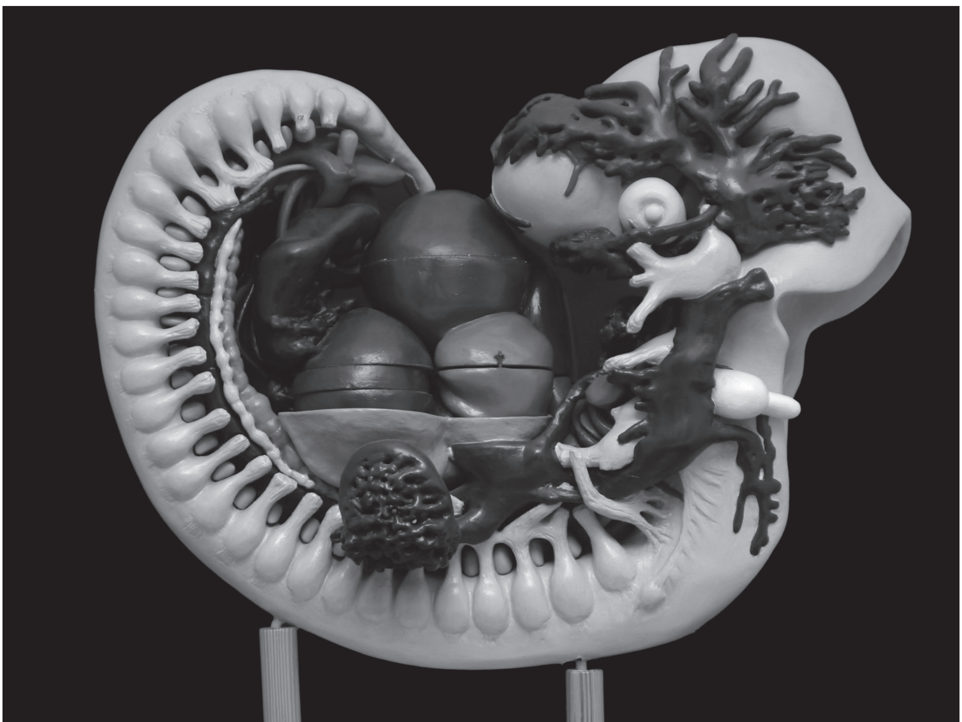

Fig. 3. The Osterloh Embryo model in left-sided (sinistral) view (hereafter photo by M. Markert)

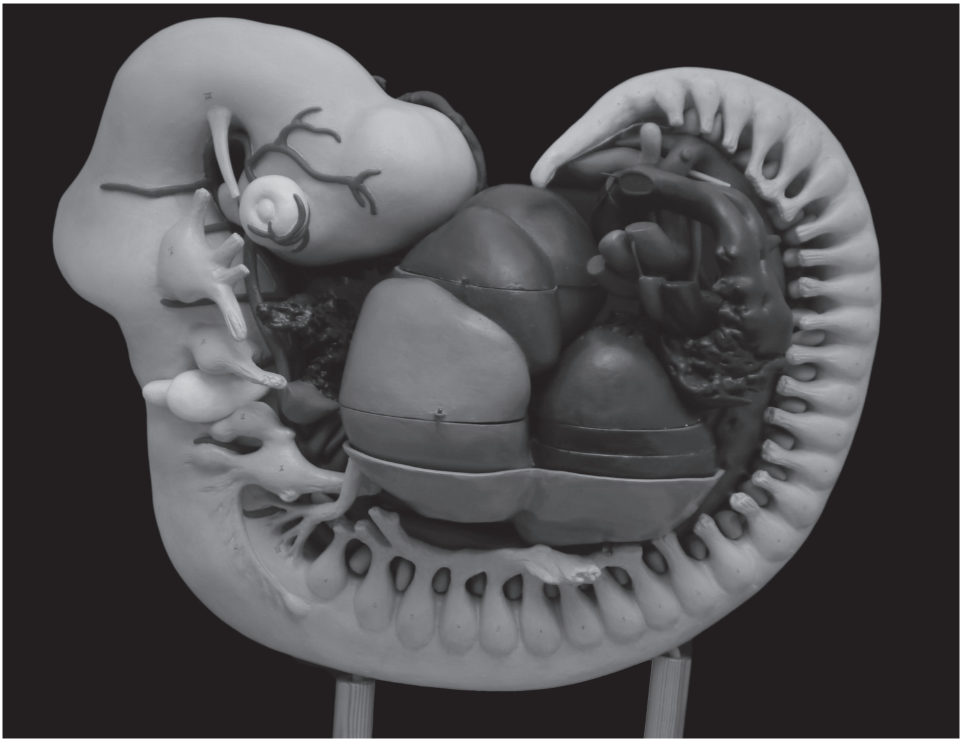

Fig. 4. The Osterloh Embryo model in right-sided (dexter) view

the end of the fourth week of development (Embryo His / Br3). The embryo has been magnified 100 times from its real size (9,6 mm) and can be taken apart to reveal inner organs and the inside of e.g. the liver and the heart (Osterloh, 1916). The model was produced from the 1920s on by the company Osterloh-Modelle in Leipzig, Germany, and only three existing copies are known today. It shows the extraordinary craftsmanship of the makers, and serves as a kind of summary in three dimensions of the recently gained detail knowledge of human embryonic anatomy.

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Epilogue

In 1977 Steven Jay Gould published his *Ontogeny and Phylogeny*, where he summarized the prehistory and history of the interplay between developmental and evolutionary biology, and also sketched a research program for the (re-)unification of these — at the time — largely independent research areas. The book became a milestone in the history of the life sciences. Now, more than thirty years after Gould's seminal publication there is an urgent need to rethink some crucial aspects of the story. As pointed out, the new integrative science, Evo-Devo has been established. Evo-Devo combines embryology, molecular biology, paleontology, and evolutionary biology along with its own methodological reflections and is about to revolutionise evolutionary theory. Yet only a few studies of the history of Evo-Devo are based on primary sources and internationally oriented. This paper fills the gap between new theoretical demands and the absence of recent historical reflections needed for the current educational landscape. Research into the visualization of the history of Evo-Devo can also clarify general methodological principles concerning the interrelationship between development and evolution.

The discussions surrounding the biogenetic law exemplifies the fertile interaction between embryology, comparative anatomy and evolutionary theory in the late 19th and early 20th 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. These discussions became important milestones in the history of evolutionary developmental biology.

Literature

Amundson R. The Changing Role of the Embryo in Evolutionary Thought: Roots of Evo-Devo. Cambridge: Cambridge University Press, 2005. 280 p.

Arthur W. The emerging conceptual framework of evolutionary developmental biology // Nature. 2002. № 415. P. 757–764.

Brandstetter Th. Embryos and Empathy: The Model Experiments of Wilhelm His // Brauckmann S., Brandt C., Thieffry D., Müller G (eds.) Graphing genes, cells, and embryos. Cultures of Seeing 3D and Beyond MPI. Gesellschaft 380, 2009. P. 123–132.

Brigandt I. Homology and heterochrony: The evolutionary embryologist Gavin Rylands de Beer (1899–1972) // Journal of Experimental Zoology. B. Molecular and Developmental Evolution. 2006. № 306. P. 317–328.

Darwin C. The descent of man, and selection in relation to sex. 2 vols. London: John Murray, 1871.

Dennett D. Darwin's dangerous idea: Evolution and the meanings of life. New York: Simon and Schuster, 1995. 585 p.

Haeckel E. Generelle Morphologie der Organismen. 2 vols. Berlin: Georg Reimer Verlag, 1866.

Haeckel E. Monographie der Kalkschwämme. 3 vols. Berlin: Georg Reimer Verlag, 1872.

Hall B.K. Evolutionary Developmental Biology (Evo-Devo): Past, Present, and Future // Evolution: Education and Outreach. 2012. Vol. 5. № 2. P. 184–193.

His W. Unsere Körperform und das physiologische Problem ihrer Entstehung. Leipzig: F.C.W. Vogel, 1874. 224 S.

Hoßfeld U., Olsson L. The road from Haeckel. The Jena tradition in evolutionary morphology and the origin of „evo-devo" // Biology and Philosophy. 2003. Vol. 18. № 2. P. 285–307.

Hoßfeld U., Olsson L., Breidbach O. (eds). Carl Gegenbaur and Evolutionary Morphology. Jena: Urban & Fischer, 2003. 198 p. (Theory in Bioscinces. Vol. 122. Hft 2/3).

Junker T. Die zweite Darwinsche Revolution. Geschichte des synthetischen Darwinismus in Deutschland 1924 bis 1950 Marburg: Basilisken-Presse, 2004. 635 S. (Acta Biohistorica. Bd. 8).

Junker T., Hoßfeld U. Die Entdeckung der Evolution. Eine revolutionäre Theorie und ihre Geschichte. 2nd ed. Darmstadt: WBG, 2009. 270 p.

Levit G.S. The roots of evo-devo in Russia: is there a characteristic "Russian tradition"? // Theory in Biosciences. 2007. Vol. 126. № 4. P. 131–148.

Levit G.S., Hoßfeld U., Olsson L. The integration of Darwinism and evolutionary morphology: Alexej Nikolajevich Sewertzoff (1866–1936) and the developmental basis of evolutionary change // Journal of Experimental Zoology. B Molecular and Developmental Evolution. 2004. № 302. P. 343–354.

Levit G.S., Hoßfeld U., Olsson L. From the "Modern synthesis" to cybernetics: Ivan Ivanovich Schmalhausen (1884–1963) and his research program for a synthesis of evolutionary and developmental biology // Journal of Experimental Zoology. B. Molecular and Developmental Evolution. 2006. № 306. P. 89–106.

Love A.C. Evolutionary morphology and evo-devo: Hierarchy and novelty // Theory in Biosciences. 2006. Vol. 124. № 3–4. P. 317–333.

Love A.C. Marine invertebrates, model organisms, and the modern synthesis: Epistemic values, evo-devo, and exclusion // Theory in Biosciences. 2009. Vol. 128. P. 19–42.

Love A.C., Raff R.A. Knowing your ancestors: Themes in the history of evo-devo // Evolution Development. 2003. Vol. 5. P. 327–330.

Mayr E., Provine W.B. (eds) The evolutionary synthesis: Perspectives on the unification of biology. Cambridge (MA); London: Harvard University Press, 1980. 487 p.

Mocek R. Wilhelm Roux — Hans Driesch. Zur Geschichte der Entwicklungsphysiologie der Tiere. Jena: Gustav Fischer Verlag, 1974. 229 S.

Mocek R. Die werdende Form. Eine Geschichte der kausalen Morphologie. Marburg: Basilisken-Presse, 1998. 579 S.

Müller F. Für Darwin. Leipzig: Wilhelm Engelmann, 1864. 91 p.

Müller G.B. Evo-devo as a discipline // Minelli A., Fusco G., Evolving Pathways: Key Themes in Evolutionary Developmental Biology. Cambridge: Cambridge University Press, 2008. P. 1–30.

Olsson L. A clash of traditions: The history of comparative and experimental embryology in Sweden as exemplified by the research of Gösta Jägersten and Sven Hörstadius // Theory in Biosciences. 2007. Vol. 126. P. 117–129.

Olsson L., Hoßfeld U. Breidbach O. Preface: Between Ernst Haeckel and the homeobox: The role of developmental biology in explaining evolution // Theory in Biosciences. 2009. Vol. 128. P. 1–5.

Olsson L., Hoßfeld U. Die Entwicklung: Die Zeit des Lebens. Ausgewählte Themen zur Geschichte der Entwicklungsbiologie // E. Höxtermann, H. Hilger (Eds) Lebenswissen. Eine Einführung in die Geschichte der Biologie. Rangsdorf: Natur & Text, 2007. S. 218–243.

Olsson L., Levit G.S., Hoßfeld U. Evolutionary Developmental Biology: Its Concepts and History with a Focus on Russian and German Contributions // Naturwissenschaften. 2010. Bd. 97. № 11. S. 951–969.

Osterloh P. Begleitheft. Modell eines menschlichen Embryos am Ende der vierten Woche (Embryo His / Br3, nat. Größe – 9,6 mm) // Vergrößerung 100fach. Leipzig. 1916. № 392.

Raff R.A., Love A.C. Kowalevsky, comparative evolutionary embryology, and the intellectual lineage of evo-devo // Journal of Experimental Zoology. B. Molecular and Developmental Evolution. 2004. № 302. P. 19–34.

Ulrich W. Ernst Haeckel: 'Generelle Morphologie', 1866 (Fortsetzung und Schluß) // Zoologische Beiträge. 1968. № 14. S. 213–311.

Uschmann G. Einige Bemerkungen zu Haeckels biogenetischem Grundgesetz // Urania. 1953. Bd. 16. № 4. S. 131–138.

Uschmann G. Geschichte der Zoologie und der zoologischen Anstalten in Jena 1779–1919. Jena: Gustav Fischer Verlag, 1959. 249 S.

История эмбриологии через линзу модели эмбриона (Embryo His / Br3), произведённого фирмой Остерло в Лейпциге

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В эпоху компьютеров и компьютерных моделей значение трёхмерных материальных моделей часто преуменьшается. Один из важных аспектов эмбриологии — анатомия развития человеческих и животных эмбрионов. В настоящей статье мы представляем исключительно ценную модель человеческого эмбриона (His / Br3, реальные размеры — 3 мм × 9,6 мм). Модель показывает эмбрион в стократном увеличении и была произведена в 30-х гг. XX столетия фирмой Остерло в Лейпциге (Германия). Модель разборная и включает много деталей, например сердце и печень, которые, в свою очередь, также разбираются. В дополнение модель демонстрирует развитие глаза, носа, внутреннего уха, конечностей и кровеносной системы. Тот факт, что эмбрион на этой стадии развития обладает органами, которые впоследствии исчезают (хвост), означает, что модель может использоваться для обсуждения биогенетического закона и других теоретических вопросов.

Ключевые слова: Э. Геккель, embryo model, фирма Остерло, Evo-Devo, эмбриологическое развитие, физиология развития, Фриц Мюллер, gastraea, дидактика в биологии.