Ernst Haeckel's Biogenetic Law (1866)

The biogenetic law is a theory of development and evolution proposed by Ernst Haeckel in Germany in the 1860s. It is one of several recapitulation theories, which posit that the stages of development for an animal embryo are the same as other animals' adult stages or forms. Commonly stated as ontogeny recapitulates phylogeny, the biogenetic law theorizes that the stages an animal embryo undergoes during development are a chronological replay of that species' past evolutionary forms. The biogenetic law states that each embryo's developmental stage represents an adult form of an evolutionary ancestor. According to the law, by studying the stages of embryological development, one is, in effect, studying the history and diversification of life on Earth. The biogenetic law implied that researchers could study evolutionary relationships between taxa by comparing the developmental stages of embryos for organisms from those taxa. Furthermore, the evidence from embryology supported the theory that all of species on Earth share a common ancestor.

Ernst Haeckel studied animals and evolution in Germany from 1834 to 1919. He proposed the biogenetic law while working at the University of Jena in Jena, Germany, in his 1866 book Generelle Morphologie der Organismen [General Morphology of the Organisms]. The publication unifies theories Haeckel proposed during his work throughout the 1850s and 1860s. Haeckel cited Johann Wolfgang von Goethe from Germany, Jean Baptiste Lamarck from France, and Charles Darwin from England as his main influences for creating the biogenetic law.

Haeckel proposed the biogenetic law after reading Charles Darwin's theories in The Origin of Species. Haeckel championed Darwin's theory of evolution in Germany and praised him for using information from embryology to help form his theory of evolution. Darwin argued that one could explain facts about embryology, such as the early similarity between embryos of different species, by looking at them in terms of evolution by natural selection. The fact that the more general characters of a taxonomic group tend to be present earlier in the embryo, while specialized and variable characters tend to manifest later in the embryo, indicated that these specialized features are the most recent changes to the ancestral form. Darwin proposed that the embryos of currently living species would look similar to the embryos of their ancestors and that embryos of different taxonomic groups look similar to each other because they share a common ancestor. Haeckel interpreted the data differently than Darwin, and he purported instead that the embryonic stages of extant species represent adult forms of their previous ancestors.

Although Haeckel cited Darwin as he proposed the biogenetic law, the two disagreed about embryology and evolution. First, Haeckel interpreted the process of evolution as progressive, following a specified path from lower to higher animals. Darwin, however, argued that evolution wasn't progressive. He also argued that embryos diverged more from one another as development progressed, rather than passing through linear stages of evolutionary ancestry. Because Haeckel argued that evolution was progressive, he also endorsed Jean Baptiste Lamarck's theory of acquired characters. Lamarck theorized that organisms could acquire or alter their characters by use and disuse of their anatomical parts, and that parents could pass on these acquired or altered characters to their offspring. Lamarck's theory competed with Darwin's of natural selection as the mechanism for evolution, but Haeckel incorporated both theories into the biogenetic law.

Haeckel proposed the biogenetic law so that researchers could use the stages of embryological development to help construct evolutionary (phylogenetic) trees. Haeckel claimed that phylogenesis, or the process by which groups of organisms diversify from one another, influenced the development (ontogeny) of embryos. He theorized that the stages in an organism's ontogeny reflected the successive changes in form, from generation to generation, of that organism's evolutionary ancestors. Many scientists saw Haeckel's work as a breakthrough in recapitulation theory because he offered a physical mechanism of development that other biologists had not proposed.

According to Haeckel, the biogenetic law depends on three assumptions. He called the first assumption the law of correspondence, which states that each stage of development in higher animals, such as humans, corresponds to adult stages of lower animals, such as fish. For instance, gill slits in early human embryos correspond to the gill slits in adult fish. The second assumption of the biogenetic law was that phylogenesis must occur by the addition of new characters to the end of the normal developmental process. Haeckel said that the early stages of different species' embryos look similar to each other because of developmental constraints present early in development. These constraints disappear towards the end of development, which allow for the addition of new characters and for subsequent evolution. The third assumption was the principle of truncation. Haeckel argued that if new characters were continuously added to the end of normal ontogeny, the length of embryonic development would eventually become longer than gestation periods of organisms in extant species. As a result, he theorized that early stages of development must be faster in higher organisms than in lower ones.

Haeckel also used the concept of truncation to explain inconsistencies between the stages of animals from different taxa. For instance, pigs and humans may look similar to each other as early embryos, but as ontogeny progresses, the embryos start to look different from one another. If embryos pass through the linear stages of their evolutionary ancestors, as Haeckel claimed, then the two embryos should go through the same stages until the pig reaches full development and the human continues through the subsequent stages of its evolutionary ancestry. However, in many cases, scientists found no such progressions. Haeckel hypothesized that truncation of ontogeny caused these inconsistencies. This principle of truncation influenced scientists in the US such as Alpheus Hyatt, Alpheus Packard, and Edward Drinker Cope.

Haeckel supported his biogenetic law with his drawings of embryos during different stages of development. In 1874, his work Anthropogenie included drawings of embryonic fish, salamanders, tortoises, chicks, pigs, cows, rabbits, and humans at different stages of development placed next to one another for comparison. Haeckel's drawings made the embryos of the different groups look almost identical in their earliest stages of development. He argued that they only become recognizable as species later in their respective developments. These similarities, according to Haeckel, demonstrated the linear progression from what he called lower forms to higher forms of animals, and he concluded that the stages recapitulated the evolutionary history of the organisms' ancestors.

Wilhelm His, professor of anatomy at the University of Basel in Basel, Switzerland, and at the University of Leipzig in Leipzig, Germany, opposed Haeckel's biogenetic law. He argued that embryologists shouldn't aim to construct phylogenetic trees and argued that embryologists should instead aim to explain development. He agreed with Haeckel that one should use causal theories to explain development, but he argued that Haeckel's theory was flawed in positing the stages of development as representations of adult ancestors. He argued the Haeckel's biogenetic law overemphasized evolution as the cause of development and exaggerated the similarities between embryos of different species. He said that there were obvious differences between the early stages of embryos of different species, and that those differences, not the similarities, were important to explain development.

In the decades after Haeckel's publication of the biogenetic law, other biologists struggled to recreate Haeckel's results. Franz Keibel, a student of Wihelm His and a professor of anatomy at the University of Strasbourg in Alsace, France, tried to recreate Haeckel's drawings from his own specimens and concluded that Haeckel had exaggerated the similarity between embryos in his drawings. Keibel therefore rejected the biogenetic law and labeled it an exaggeration of the truth. In 1897, Keibel published this conclusion in the first volume of Normentafeln zur Entwicklungsgeschichte der Wirbelthiere (Standard Panels to the Developmental History of the Verterbra).

Furthermore, many scientists adopted a competing theory in the beginning of the twentieth century. In 1828, Karl Ernst von Baer at University of Königsberg in Königsberg, Prussia, had proposed what researchers later called von Baer's laws of embryology. Von Baer formulated these laws to discredit conception of recapitulation theory published in 1811 by Johann Friedrich Meckel. In his laws, von Baer stated that the more general characters of a taxonomic group appear earlier in an animal embryo than the specialized characters do. He argued that rather than animals passing through successive stages of other adult animals, they diverge from one another as development progresses. Therefore, he concluded, the stages embryos pass through during ontogeny never represent adult forms of other animals; they only represent embryonic stages of other animals. This conception was part of Darwin's 1859 account of ontogeny in The Origin of Species. Although von Baer's theory was overshadowed by recapitulation theory for most of the nineteenth century, scientists in the twentieth century began to adopt von Baer's view as the more accurate representation of development.

Haeckel's biogenetic law was further discredited by the results of experimental embryologists in the early twentieth century. Researchers abandoned Haeckel's theory when they couldn't confirm his observations. Embryologists showed that cases of recapitulation were less prevalent than were the inconsistencies between the developmental stages of normal organisms from different species.

Sources

1. von Baer, Karl Ernst. Über Entwickelungsgeschichte der Thiere. Beobachtung und reflexion [On the Developmental History of the Animals. Observations and Reflections]. Königsberg: 1828. http://www.biodiversitylibrary.org/item/28306 (Accessed December 3, 2013).
2. Cope, Edward. ”On the Origin of Genera.” Proceedings of the Academy of Natural Sciences 20 (1868): 242–300. In Edward Dinker Cope, The Origin of the Fittest. New York: D. Appleton and Co., 1887: 41–123. http://www.biodiversitylibrary.org/item/75034#page/67/mode/1up (Accessed April 26, 2012).
3. Cope, Edward. ”The Laws of Organic Development.” The American Naturalist 5 (1871): 593–608. http://biodiversitylibrary.org/page/40869958#page/613/mode/1up (Accessed December 3, 2013).
4. Darwin, Charles R. On the Origin of Species by Means of Natural Selection, or the Preservation Of Favoured Races in the Struggle for Life. London: John Murray Publishing House, 1859. http://darwin-online.org.uk/content/frameset?pageseq=1&itemID=F373&viewtype=text (Accessed December 3, 2013).
5. Gould, Stephen J. Ontogeny and Phylogeny. Cambridge: Harvard University Press, 1977.
6. Gould, Stephen J. The Structure of Evolutionary Theory. Cambridge: Harvard University Press, 2002.
7. Haeckel, Ernst. Generelle morphologie der organismen [General Morphology of the Organisms]. Berlin: G. Reimer, 1866. http://www.biodiversitylibrary.org/item/22319#page/11/mode/1up (Accessed December 3, 2013).
8. Haeckel, Ernst. Anthropogenie: oder, Entwickelungsgeschichte des Menschen. Keimes—und Stammesgeschichte [Anthropogeny, or the Evolutionary History of Humans]. Vol. 1. Leibzig: Engelmann, 1877. http://biodiversitylibrary.org/page/3146520 (Accessed December 13, 2013).
9. His, Wilhelm. ”On the Principles of Animal Morphology: Letter to John Murray.” Proceedings of the Royal Society 15 (1888): 287–98.
10. Hopwood, Nick. ”A History of Normal Plates, Tables, and Stages in Vertebrate Embryology.” International Journal of Developmental Biology 51 (2007): 1–26.
11. Keibel, Franz. Normentafeln zur Entwicklungsgeschichte der Wirbelthiere [Standard Panels to the Developmental History of the Verterbra]. Jena: G. Fischer, 1897. http://biodiversitylibrary.org/page/8355515 (Accessed December 3, 2013).
12. Lamarck, John Baptiste. Philosophie Zoologique [Zoological Philosophy]. Vol. 1. Paris: Duminil-Lesueur, 1830. http://biodiversitylibrary.org/page/33947063 (Accessed December 3, 2013).
13. Lamarck, John Baptiste. Histoire naturelle des animaux sans vertébres [Natural History of Invertebrate Animals]. Paris: J.B. Bailliére, 1838. https://archive.org/stream/histoirenaturell051838lama#page/n7/mode/2up (Accessed December 3, 2013).
14. Maienschein, Jane. ”Cell Lineage, Ancestral Reminiscence, and the Biogenetic Law.” Journal of the History of Biology 1 (1978): 129–58.

15. Meckel, Johan Friedrich. Beyträge zur vergleichenden Anatomie [Contributions to Comparative Anatomy]. Halle: Reclam, 1808. https://archive.org/stream/beytrgezurvergl00meckgoog#page/n11/mode/2up (Accessed December 3, 2013).
16. Renard, Ruth. ”The Problem of the Organic Individual: Ernst Haeckel and the Development of the Biogenetic Law.” Journal of the History of Biology 14 (1981): 249–75.