

Ontogeny and Phylogeny (1977), by Stephen Jay Gould

Ontogeny and Phylogeny is a book published in 1977, in which the author Stephen J. Gould, who worked in the US, tells a history of the theory of recapitulation. A theory of recapitulation aims to explain the relationship between the embryonic development of an organism (ontogeny) and the evolution of that organism's species (phylogeny). Although there are several variations of recapitulationist theories, most claim that during embryonic development an organism repeats the adult stages of organisms from those species in its evolutionary history. Gould suggests that, although fewer biologists invoked recapitulation theories in the twentieth century compared to those in the nineteenth and eighteenth centuries, some aspects of the theory of recapitulation remained important for understanding evolution. Gould notes that the concepts of acceleration and retardation during development entail that changes in developmental timing (heterochrony) can result in a trait appearing either earlier or later than normal in developmental processes. Gould argues that these changes in the timing of embryonic development provide the raw materials or novelties upon which natural selection acts.

Gould wrote *Ontogeny and Phylogeny* while working at Harvard University in Cambridge, Massachusetts, as a professor of zoology. He had studied the relationship between ontogeny and phylogeny early in primary school in the New York City public schools. One of his colleagues at the American Museum of Natural History, Ernst Mayr, in the late 1970s encouraged him to write a book on the subject.

Gould noted that Ernst Haeckel in Germany proposed an 1866 recapitulation theory that he termed the biogenetic law, and that biologists appealed to the law into the early decades of the twentieth century, after which time experimental evidence disconfirmed the law. Gould argues that the dismissal of Haeckel's biogenetic law led to a more general dismissal of the theory of recapitulation. Therefore, the bad reputation attached to the theory of recapitulation impacted the way scholars eventually theorized about developmental processes as part of the mechanism of evolution.

Ontogeny and Phylogeny is divided into two parts. The first part is entitled "Recapitulation" and reconstructs the history of the theory of recapitulation from Greek roots to Ernst Haeckel's biogenetic law and to its demise in the first half of the twentieth century. The second part is entitled "Heterochrony and Paedomorphosis." In this section, Gould proposes his own theories about the relationship between ontogeny and phylogeny and the way developmental processes help to explain evolution.

Part one of *Ontogeny and Phylogeny* begins with chapter two, "The Analogistic Tradition from Anaximander to Bonnet". In this chapter, Gould describes pre-recapitulation theories as various ways of paralleling ontogeny with the hierarchies of life. For example, some categorized the hierarchy of things as progressing from mere matter, to unconscious life, to the conscious animal, to the rational human. The ontogeny of a human repeats this hierarchy. Starting from the bottom of the hierarchy, the human begins as unformed, unconscious matter and then progresses to form complex living matter. Later in development, the human fetus resembles an animal and then finally progresses to be a rational human. For instance, Aristotle in ancient Greece described the sequence of development in a human embryo as analogous to a sequence of progressively higher souls unfolding inside the organism as it develops, starting with the vegetative or nutritive soul, then progressing to the animal or sensitive soul, and then finally to the human or rational soul.

Next, in the same section, Gould focuses on recapitulation theories of the sixteenth century and describes how embryologists attempted to explain ontogeny through theories either of preformationism or of epigenesis. Preformationists stated that structures of adults were preformed in the sex cell, and merely unfolded from prebuilt complexity. In contrast, epigenesists hypothesized that organisms began formless and subsequently increased in complexity and form during development. Gould states that historians had characterized preformationism in an attempt to retell the history of embryology as a good guy (epigenesicists) and bad guy (preformationists) narrative in which epigenesists triumphed. However, Gould says that preformationist theories were much more rational and respectable than historians portrayed them.

In Chapter three, entitled "Transcendental Origins, 1793 - 1860," Gould describes the triumph of epigenesis over preformationism and the subsequent rise of the theory of recapitulation in the

movement called Naturphilosophie (philosophy of nature) in Germany during the early nineteenth century. Embryologists claimed that physical laws could explain all natural phenomena, and that motion was the only irreducible property. From these premises, recapitulation became a central theory because it relied on purely natural explanations. Gould describes in detail two contemporary leading theories of recapitulation by Lorenz Oken and Johann F. Meckel, both located in Germany. Meckel stated in the title of his 1811 essay "Entwurf einer Darstellung der zwischen dem Embryozustande der höheren Tiere und dem permanenten der niederen stattfindenden Parallele" (Sketch of the Portrayal of the Parallels that Exist Between the Embryonic Stages of Higher Animals and the Adults of Lower Animals) that early embryonic stages of so-called higher animals somehow related to the adult stages of lower animals. Oken, in his 1843 *Lehrbuch der Naturphilosophie* (Textbook of Natural Philosophy), classified animals based on the linear addition of organs as they developed in the animals.

Gould next discusses Karl E. von Baer, who worked on embryos in Dorpat, later Tartu, Estonia. Gould shows that von Baer argued against the theory of recapitulation. Von Baer stated that many of the features present in embryonic stages are not apparent in the adult, and therefore one could not claim any correspondence between embryos belonging to different species. Von Baer's 1828 laws of embryology claim that embryos of one species can only resemble the embryonic form of ancestors, but never their ancestors' adult forms. Von Baer argues that organisms from different species develop from a common general form and then diverge from one another in a branching manner as development proceeds.

Chapter four, "Evolutionary Triumph, 1859-1900", discusses the period in which Charles Darwin introduced the theory of evolution. Before this theory, biologists struggled to explain the patterns described in Meckel's recapitulation theory. The claim that life evolved from a common ancestor enabled biologists to view embryonic stages of animals as the actual product of those animals' ancestries. Scientists developed at least two interpretations of the relationship between ontogeny and phylogeny. First, some biologists interpreted evolution with von Baer's laws of embryology. This interpretation described development as progressing from the general characters of a large group to the specialized characteristics of that organism's species. The second interpretation described embryonic stages as the adult forms of our ancestors. Gould notes that Darwin's embryological arguments for evolution in *Origin of Species* relied on von Baer's laws.

Gould then describes how the second interpretation presupposed two claims. First, evolutionary changes must occur through the addition of traits to the end of ontogeny, a claim called the principle of terminal addition. Second, there must be a mechanism that shortens ontogeny across generations, otherwise development would be much longer than what we observe today, a claim called the principle of condensation. In the latter half of the nineteenth century, many theories attempted to explain how terminal addition and condensation occurred.

In the last part of chapter four, Gould discusses Ernst Haeckel's theory of recapitulation, which had an evolutionary perspective. Evolutionary recapitulation differed from other forms of recapitulation as it integrates the theory of common ancestry for all organisms. Haeckel aimed to reconstruct phylogenetic lineages of organisms and used the parallels between ontogeny and phylogeny as evidence for his hypothesized lineages. Haeckel's biogenetic law claimed that phylogeny, which is the evolution and diversification of a species, physically caused the embryonic stages in animals' development. Moreover, Haeckel addressed the principles of terminal addition and condensation as the mechanics of recapitulation. Gould emphasizes how other biologists such as Edward D. Cope and Alpheus Hyatt, both in the US, independently proposed the biogenetic law. All of them proposed similar principles and laws of acceleration and retardation. Gould ends chapter four describing how by the late nineteenth century, von Baer's laws of embryology fared poorly amongst scientists, whereas Haeckel's biogenetic law gained popularity.

Chapter five, "Pervasive Influence," provides excerpts from doctors, poets, writers, physicists, and educators who wrote about recapitulation. Gould speculates that recapitulation was not just influential to evolutionary and developmental biologists, but also to much of society.

In "Decline, Fall, and Generalization," Gould describes the decline of the biogenetic law in the first half of the twentieth century, and he identifies several factors influencing the decline. First, he

notes that the empirical critiques addressing acceleration and retardation made the biogenetic law untenable. Then, Gould says that in the 1920s Walter Garstang, in UK, emphasized a contradiction in the biogenetic law: that late stages of development sometimes retain the juvenile characters of the ancestors. Garstang called this phenomena paedomorphosis, and he described its occurrence in the salamanders from Mexico. Garstang argued that, as the biogenetic law required that adult stages of ancestors appear in the juvenile stages of development, it was disconfirmed by evidence of juvenile features of ancestors expressed in the adult forms of organisms. Additionally, Gould notes the difficulties that arose for the biogenetic law once Gregor Mendel's 1865 theory of genetics and experimental embryology became popular. According to Gould, once new causal explanations accounted for variations in the features of organisms within the same species, the biogenetic law became irrelevant.

Section two of *Ontogeny and Phylogeny* has four chapters. The first two chapters in this section, chapters seven and eight in the book, are entitled "Heterochrony and the Parallel of Ontogeny and Phylogeny" and "The Ecological and Evolutionary Significance of Heterochrony". In these chapters, Gould emphasizes the mechanics of developmental timing rather than the results of those processes. He argues that, once Haeckel's biogenetic law declined in popularity, it prompted the design of many complex theories about the connections between ontogeny and phylogeny, theories that focused on the results of changes in developmental timing, recapitulation and paedomorphosis, but did not focus on its mechanisms, acceleration and retardation.

Gould argues that scientists should study the processes of developmental timing. He identifies two processes causing recapitulation and paedomorphosis: acceleration and retardation of development. Furthermore, the ubiquitous presence of these processes in development shows that heterochrony constitutes the mechanics of evolution, as it can result in different evolutionary phenomena such as the number of offspring an organism has or the age at which an organism reproduces.

In "Progenesis and Neoteny" and "Human Evolution," Gould explains progenesis and neoteny. Progenesis occurs when the sexual maturation of an organism still in a juvenile stage accelerates. For example, some salamanders are able to reproduce during their larval life. Gould argues that neoteny and progenesis are adaptations to different ecological environments. Progenesis enables species to reproduce quickly and in large numbers. Neoteny, on the other hand, causes species to reproduce slowly and in small numbers. Progenesis can result in the evolution of new taxa, because it can relax the developmental constraints that later arise in the development of organisms. Gould points to neoteny as an important process in the development of complex social and cerebral behavior in the higher vertebrates. He says that the ability for an organism to delay its growth can lead to features that would support complex social and cerebral behaviors. For instance, rapid growth of the brain later in the development of humans could support complex cerebral functions. Gould claims that neoteny is the most important factor of human evolution.

In the decades that followed its publication, *Ontogeny and Phylogeny* became widely cited within the evolutionary and developmental sciences. It helped revive research on acceleration and retardation and sparked research about paedomorphosis as a possible factor affecting the evolution of the human lineage. Moreover, *Ontogeny and Phylogeny*, along with other work by Gould, such as "The Spandrels of San Marco and the Panglossian Paradigm" is often credited for influencing the rise of a biological approach called evolutionary developmental biology or evo-devo, which worked to integrate evolutionary and developmental biology.

Sources

1. Aristotle. *On the Generation of Animals*. Trans. Arthur Platt under the Editorship of J.A. Smith and W.D. Ross as Volume V of *The Works of Aristotle Translated into English* Oxford: Clarendon Press, 1912. <https://ebooks.adelaide.edu.au/a/aristotle/generation/index.html> (Accessed October 9, 2014).
2. Cope, Edward. *The Primary Factors of Organic Evolution*. Chicago: Open Court Publishing, 1896. <http://www.biodiversitylibrary.org/page/1959466> (Accessed April 26, 2014).

3. Darwin, Charles. *On the Origin of Species by Means of Natural Selection*. London: John Murray, 1859. <http://dx.doi.org/10.5962/bhl.title.68064> (Accessed October 9, 2014).
4. Garstang, Walter. "The Theory of Recapitulation: A Critical Restatement of the Biogenetic Law." *Zoological Journal of the Linnaean Society* 35 (1922): 81-101.
5. Gorman, James. "The History of an Idea." *New York Times*, November 20, 1977. <http://www.nytimes.com/books/97/11/09/home/gould-darwin.html> (Accessed February 16, 2013).
6. Gould, Stephen J. *Ever Since Darwin*. New York: Norton & Company, 1977.
7. Gould, Stephen J. *Ontogeny and Phylogeny*. Cambridge: Harvard University Press, 1977. <http://www.sjgarchive.org/library/ontogeny.html> (Accessed 17 April 2014).
8. 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 May 4, 2012).
9. Hyatt, Alpheus. "Cycle in the Life of the Individual (Ontogeny) and in the Evolution of Its Own Group (Phylogeny)." *Science* 5 (1897): 161-71. <http://www.jstor.org/stable/20020691> (Accessed October 9, 2014).
10. McKinney, Michael and Kenneth McNamara. "Heterochrony, Disparity, and Macroevolution." *Paleobiology* 31 (2005): 17-26.
11. Meckel, Johann Friedrich. "Entwurf einer Darstellung der zwischen dem Embryozustande der höheren Thiere und dem permanenten der niederen stattfindenden Parallele." [Sketch of the Portrayal of the Parallels that Exist Between the Embryonic Stages of Higher Animals and the Adults of Lower Animals]. In *Beyträge zur Vergleichenden Anatomie* [Contributions to Comparative Anatomy] Vol. 2. Ed. Johann Friedrich Meckel. Leipzig: Reclam, 1811: 1-60.
12. Mendel, Gregor Johann. "Versuche über Pflanzen-Hybriden" [Experiments Concerning Plant Hybrids]" [1866]. *Verhandlungen des naturforschenden Vereines in Brünn* [Proceedings of the Natural History Society of Brünn] IV (1865): 3-47. Reprinted in *Fundamenta Genetica*, ed. Jaroslav Kříženecký, 15-56. Prague: Czech Academy of Sciences, 1966. <http://www.mendelweb.org/Mendel.html> (Accessed April 17, 2014).
13. Oken, Lorenz. *Lehrbuch der Naturphilosophie*. Zürich: Schultheß, 1843. <https://archive.org/details/lehrbuchdernatu04okengooq> (Accessed April 17, 2014).
14. von Baer, Karl Ernst. *Über Entwicklungsgeschichte der Thiere. Beobachtung und Reflexion* [On the Developmental History of Animals. Observation and Reflection]. Königsberg: Bornträger, 1828. <http://babel.hathitrust.org/cgi/pt?id=inu.32000003298751;page=root;view=1up;size=100;seq=7;orient=0> (Accessed October 3, 2012).
15. Wake, David. "Shape, Form, Development, Ecology, Genetics, and Evolution." *Paleobiology* 4 (1978): 96-9.