

## BOOK REVIEW

# Ontogeny does not recapitulate phylogeny, it creates phylogeny: a review of *The Tragic Sense of Life: Ernst Haeckel and the Struggle over Evolutionary Thought*, by Robert J. Richards

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**The Tragic Sense of Life: Ernst Haeckel and the Struggle over Evolutionary Thought**, Robert J. Richards, 2009, University of Chicago Press, Chicago, xx+551pp. Paper: ISBN 978-0-226-71216-1 US\$25.00.

Then he [Jung] laid his hand out flat against her skin and made the shape of the child inside.

“You ever hear the phrase *ontogeny recapitulates phylogeny*?” he said.

“I’m sure I’d remember if I had,” Emma laughed. “I couldn’t begin to tell you what it means.”

“Man called *Haeckel*. Ernst Haeckel. Biologist. German. Long dead—but controversial in his time. We had to study him at university . . . a disciple of Darwin’s. Disciple and extrapolator. Went a few steps beyond the master, so to speak. Such as: *ontogeny recapitulates phylogeny*.”

“Heavens—what huge words!”

“*Ontogeny—the origin and development of the individual*,” pronounced Jung tapping out [the words] on Emma’s stomach. “Like your little fish in here,” he added.

“Haeckel said: *ontogeny recapitulates phylogeny*—but what he should have said is *ontogeny repeats phylogeny* . . .”

“As [the fertilized egg] divides and multiplies, what it is doing is forming a mass of cells—an *unorganized* mass, not unlike a sponge.” . . . “So . . . it passes on through stages that resemble a jellyfish.” . . .

“And yet, there’s more to be had from Haeckel’s theory than mere biology . . .”

“No, Carl Gustav. No. Not more. I’m tired. It’s after two o’clock in the morning.”

Exchange between Carl Jung and his pregnant wife Emma as told in *Pilgrim* by Timothy Findlay (1999, pp. 288–291).

Having first appeared in hardcover in June 2008, release in August 2009 of a paperback printing of *The Tragic Sense of Life: Ernst Haeckel and the Struggle over Evolutionary Thought* follows a pattern established by the University of Chicago Press (UCP), a pattern that makes informed and informative books available at bargain-basement prices.

This authoritative “intellectual biography” of Ernst Haeckel (1834–1919) by the historian and philosopher of science and psychology Robert Richards has been the subject of several reviews. Perhaps the most interesting for our purposes is that by Gliboff (2009). Why single out this review? Because Gliboff’s own book (Gliboff 2008) includes an informed and extensive discussion of the influence on Haeckel of H. G. Bronn, the German paleontologist who supervised the translation into German of Darwin’s *On the Origin of Species*. Gliboff’s book has been reviewed (Bowler 2009; Meyer 2009) and the two books compared in a review by Lynn Nyhart, a noted historian of German morphology and morphologists (Nyhart 2009) (A third book-length treatment of Haeckel is also available; Di Gregorio 2005). In comparing “Richards’s emphasis on charisma and passion” with “Gliboff’s overall

picture of scientific advance,” Nyhart (2009) contrasts how these historians “have chosen two radically different strategies to understanding Haeckel’s place in German evolutionism . . .” (pp. 1170–1171).

Why this interest in a dead German white male whom the UCP tells us in an advertising blurb “is better known as a divisive figure than as a pioneering biologist.” One reason alone is sufficient. Ernst Haeckel was the preeminent German, European, indeed international proponent and disciple, propagandist, and popularizer of Darwin’s theory of evolution by natural selection. Haeckel’s influence, which began in 1864, was fostered and enhanced by Haeckel himself until his death 55 years later, and has been continued in virtually every evolutionary and introductory biology textbook even since.

Steeped as he is in German Romanticism, knowledgeable as he is in the origins of evolutionary theory, and skilled as he is as a historical researcher and consummate writer, we can all be grateful that Robert Richards devoted 15 years to Haeckel and all things Haeckelian. The result is a brilliantly written biography based on exhaustive analysis of primary literature and an important reevaluation of the position in the history of embryology and evolution into which Haeckel has been placed (thrust?) in E. S. Russell’s *Form and Function: A Contribution to the History of Animal Morphology*, written almost a century ago (Russell 1916). Haeckel has been tackled by researchers from many fields including historians and philosophers of science interested in grand theories, biologists investigating the relations between embryonic development and evolution, and political scientists exploring whether Haeckel’s philosophy (monism) played a role in the rise of the Nazi party (Richards 2007 argues it did not).

In this short review of Richards’ book I concentrate on Haeckel’s role in the history of the interaction between embryology and evolution, or ontogeny and phylogeny to use the terms coined by Haeckel. This relationship, captured by Haeckel’s sobriquet “ontogeny recapitulates phylogeny,” resonate in many avenues of human creativity, including fiction, as elegantly illustrated in the epigraph. As a second example from a major treatise *The Science of Life* published in 1934, father and son H. G. and G. P. Wells and Julian Huxley wrote that:

Tens of thousands of animals do recapitulate the past during their development . . . and in none of these tens of thousands of cases is this departure intelligible save on the view that in so doing they are repeating phases that were once final forms in the earliest evolution of the race

(Wells et al. 1934, p. 369).

Richards places Haeckel firmly in the German Romantic Movement that gelled around a remarkable generation of German scholars, including the morphologist, poet, philosopher, and polymath, Johann von Goethe (1749–1832), the

explorer, naturalist, and one of the founders of biogeography, Alexander von Humboldt (1769–1859), the botanist and co-founder of the cell theory, Matthias Schleiden (1804–1881), and others. In developing his vision of life, Haeckel used embryology, paleontology, evolution, and systematics to substitute ancestors for archetypes and to replace the progression of ideal forms with evolutionary sequences repeated in the embryonic development of every new individual, all anchored in uniform causes and the philosophical framework that became known as monism.

Sorting out how concepts such as the archetype were viewed and used by Haeckel and Darwin is no easy task. In revising an interpretative tradition initiated by Russell (1916), Richards interprets the evidence as showing both Haeckel and Darwin as having been influenced by earlier research in transcendental morphology and embryology. Most other analyses, such as Gliboff (2008), situate Haeckel but not Darwin within German idealistic morphology.

Richards (and Gliboff) provides evidence that Haeckel followed the interpretations of evolution (and used similar terminology) to that developed and published by H. G. Bronn (1800–1862) the German paleontologist who supervised the translation into German of Darwin’s “*On the Origin of Species*.” At Darwin’s invitation Bronn added his own comments, notes and a closing chapter, although the latter placed Darwin’s natural selection in the light of Bronn’s own views, which required separate creations for the origin of new groups. Having read and adopted Bronn’s supervised translation of *The Origin of Species*, Haeckel adopted Darwin’s theory, first in his 1862 treatise on the systematics and speciation of radiolarians (Haeckel 1862), then in a lecture delivered in Settin in 1864 (Haeckel 1864).

Haeckel spent between 1861 and 1866 developing an individual approach to evolution, embryology, and morphology, all wrapped in the philosophical framework that became known as monism. On July 9, 1864 Haeckel wrote to Charles Darwin:

Of all the books I have ever read, not a single one has come even close to making such an overpowering and lasting impression on me, as your theory of the evolution of species . . . Since then your theory—I can say without exaggerating—has occupied my mind every day.

(Richards 2007, p. 283)

Haeckel’s treatise *Generelle Morphologie der Organismen* (*General Morphology of Organisms: Broad Principles of Organic Forms and Sciences, Founded by the Mechanically Reformed by Charles Darwin Theory of Descent. Volume 1: General Anatomy. Volume 2: General history*) was published in 1866 (Haeckel 1866). This magnum opus was thought out, written and printed within a year—rather like a PhD thesis: “It was written and printed in less than a year. I lived then

quite like a hermit, allowing myself barely 3–4 h sleep daily, and worked all day and half the night. I lived in such strict asceticism that I must really be amazed to stand alive and healthy before you today.”

Haeckel's evolutionary views were balanced, on the one hand not invoking archetypes but seeing the record of ancestry in embryos, and on the other, finding a place for adaptation in the generation of diversity. Haeckel set his own course, neither adopting any of the forms of orthogenesis (directed evolution) popular at the time, nor embracing the mechanistic embryology developing under the hands of fellow German embryologists—Wilhelm His, August Weismann, and Wilhelm Roux.

With his emphasis on natural selection, Haeckel has sometimes been described as more Darwinian than Darwin. Curiously, at least it is curious in hindsight, many in the 20th century saw Haeckel as a Lamarckian, misreading Haeckel's use of “ontogeny recapitulates phylogeny.” As Richards' emphasizes, Haeckel recognized various types of variation but not Lamarckian inheritance. Haeckel regarded heredity and adaptation as the “two mechanical causes of evolution” (Haeckel 1876, vol. 1, p. 1) and traced these “causes” to Lamarck but, as Richards's documents with considerable evidence, Haeckel held Darwinian views on shared organismal descent, the role of natural selection in hereditary change, and the importance of variation and adaptation.

Recapitulation as developed by Haeckel was neither absolute nor complete. Only the phylogenetically oldest animal embryonic stages were preserved in the development of extant vertebrate embryos. In 1866, Haeckel introduced the concept of caenogenesis to cover those situations in which recapitulation of phylogeny in ontogeny was obscured because of larval adaptations or the displacement of embryonic or larval stages in time or space during ontogeny. For Haeckel, “The laws of inheritance and adaptation . . . are completely sufficient to explain this exceedingly important and interesting phenomenon, which may be briefly designated as the *parallelism of individual, paleontological and of systematic development*” (Haeckel 1876, vol. 1, p. 313, emphasis in the original German). From his studies on larval forms, Garstang (1922) provided the modern context: “ontogeny does not recapitulate phylogeny, it creates it” (pp. 21, 81; and see Hall 2000).

Many of us, myself included, took Gould's (1977) interpretation of Haeckelian recapitulation as requiring endless terminal additions (and/or preservation of the adult forms of ancestors) to (in) ancestral yet evolving developmental sequences. A much closer reading of Haeckel shows that Haeckel did not advocate terminal addition.

Systematics, paleontology, and embryology informed Haeckel's trees, which have for almost a century and a half all been interpreted as phylogenetic trees. Contrary interpreta-

tions exist, however. In a detailed evaluation of how Haeckel built his phylogenetic trees, Dayrat (2003) concluding that Haeckel's trees were genealogical and his view of phylogeny informed more by the Great Scale of Being than by phylogenetic change; animals ordered from lowest to highest. Although Haeckel's trees are continually and continuously depicted as phylogenetic, Dayrat emphasizes that: “Haeckel never called any of his hundreds of trees a phylogeny or a phylogenetic tree. Haeckel's trees were genealogical and were distinct from what he called a phylogeny . . . his genealogical trees were not Darwinian” (p. 515). None, according to Dayrat were the branching trees of life or cladograms constructed today.

Richards' challenges this interpretation of the nature of Haeckel's trees: Haeckel distinguished trees with a major trunk and few side branches—his genealogical trees constructed by linking a chain of ancestors—from “stem trees” with their many branches depicting phylogenetic relationships between groups of organisms (figures 5.3 and 5.10 in Richards; see also Rieppel 2010 on the same point). This important distinction between genealogical and phylogenetic trees constructed by Haeckel is only one of the many interpretive insights important for those discussing the history of phylogenetic analysis. In considering that all life may have arisen from a single source Haeckel refers to a “monophyletic stem-tree of organisms” (Richards, p. 138), a clear indication of the phylogenetic thinking behind his stem trees.

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