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BOOK REVIEW

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Turtles, monsters and the revised evolutionary theory

Evolutionary theory is incomplete. That claim has been made several times since Darwin's 1859 publication of *On the Origin of Species*—specially between those studying paleontology and development (e.g., Alpheus Hyatt, Richard Owen, and more recently Stephen J. Gould; Amundson, 2005; Gould, 1977; Pfeifer, 1965)—but recently a growing movement has gained space on scientific and general public forums calling for an Extended Evolutionary Synthesis of Evolution (Laland et al., 2015; Pigliucci & Finkelman, 2014). Its supporters argue that the Modern Synthesis—developed during the first half of the 20th century—leaves out of the picture certain processes related to ontogenetic development (but not only those; for a summary see Laland et al., 2015), that have the potential to causally explain some evolutionary events poorly addressed by the microevolution centered view of the Modern Synthesis.

In this context, Olivier Rieppel's *Turtles as Hopeful Monsters* joins the movement to increase those claims. The title may be slightly misleading: the book is not about turtles —although they play a very important role in the argument, only the last two chapters are "turtle-focused"—but about the last concept, the "Hopeful Monsters." The author provides a very detailed historical and philosophical account of how early critics of Darwin's theory saw its two basic processes, mutation and natural selection, as insufficient to explain all evolutionary events.

The term Hopeful Monster was coined by Richard Goldschmidt, a German–Jewish geneticist who spent the last part of his career at the University of California, Berkeley, studying development, genetics, and evolution. A "monstrosity," according to Goldschmidt (1940), is a phenotypic alteration that develops in a mutant individual, such as a Manx cat with truncated tail vertebrae. For this individual, the mutation does not generate an advantage (although it may not be disadvantageous, also), hence, it is just a monster. However, the same monstrosity in a non-bird dinosaur, say an *Archaeopteryx* mutant, may result in a rearrangement of the tail feathers, improving its flight capacity and its fitness. The mutant *Archaeopteryx* is, thus, a hopeful monster.

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This kind of mutation should occur early in ontogeny, reprogramming the developmental pathway while the embryo is not well-differentiated yet, resulting in a distinct adult morphology. As such, when comparing adults they appear to emerge in a "single step," that is, shortened tail offspring generated by normal tailed parents. This creates a gap between the "ancestral"—long tail—and the "descendant"—short tail—forms. The explanation of the emergence of novel structures by reprogramming developmental pathways is called "emergentist paradigm" by Rieppel (p. 124). In contrast, the Modern Synthesis embraces the so-called transformationist paradigm, which explains morphological evolution in a gradual transition between small steps. There can be no gaps in this process.

These contrasting views recall the distinction between structuralists and functionalists well developed by Ron Amundson (2005). In Rieppel's book, the emergentist paradigm sees structures coming before—and, hence, determining—functions, whereas in for the transformationists the opposite is true: function shapes structures. On Amundson's account, those supposedly incommensurable views were contrasted several times before Darwin's *Origin*, and succeeded each other in dominating the predominant view of nature. Along the exciting and easy reading 216 pages, Rieppel presents his view on how this transformationist versus emergentist explanations also shaped the debate about morphological evolution after Darwin's publication, using the turtle shell as the prime example.

Briefly, two competing hypotheses have been raised to explain the unique body plan of turtles (Rieppel, 2001). The first one considers the carapace (the dorsal portion of the shell) as an endoskeletal structure, derived from the cartilaginous precursors of the dorsal ribs and vertebrae. The second posits an exoskeletal nature for it, in which the ribs and vertebrae would fuse to overlying dermal ossifications, the osteoderms. The latter view is related to what Rieppel calls a Polka Dot Turtle Ancestor. This would be a hypothetical ancestor, that would explain the *transition* from a shell-less reptile to a turtle, through a *gradual* accumulation of osteoderms on its back. This hypothetical ancestor has been called to bridge the gap in the fossil record a couple of times during the last three decades (e.g., Joyce et al., 2009; Lee, 1996).

The big problem is that, since at least the end of the 19th century, studies on the development of the carapace (e.g., Rathke, 1848) show that the ribs and vertebrae in the turtle trunk never fuse with dermal ossifications, supporting the first hypothesis. That means that, even with evidence to the contrary, several researchers have favored the more *mainstream* transformationist view.

Rieppel's new book presents a view of "science facts" as social constructs, building on Ludwik Fleck's concept of *thought style* to explain why sometimes scientists favor one view in spite of another and how it refrains the community of thinking outside this box of knowledge. The Modern Synthesis can be viewed as one of these boxes (or circles, in Fleck's terminology), limiting our thoughts about how morphological evolution is realized through small and gradual steps, even when the sudden emergence of a new structure—like the mutant Manx cat short tails or the turtle carapace—seems more likely. According to Rieppel (p. 161) "there is no question that Darwinian evolution through variation and natural selection [. . .] does occur, but the question remains whether this is the only possible way of evolutionary transformation." The book highlights that it may be time to embrace the hopeful monsters out there and revisit the "dogmas" of Evolutionary Theory.

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