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REVIEW

The Major Transitions in Evolution Revisited

edited by Brett Calcott and Kim Sterelny Cambridge (MA): MIT Press, 2011. 319 pages

reviewed by Derek Turner

In 1995, with the publication of their book *The Major Transitions in Evolution* (1995a), John Maynard Smith and Eörs Szathmáry introduced a new way of thinking about the "big picture" of the history of life on Earth. The major transitions they focused on all involved "changes in the evolutionary process itself," as Brett Calcott and Kim Sterelny put it in their introduction to this splendid collection of papers. For example, the evolution of sexual reproduction—one of the transitions that Maynard Smith and Szathmáry thought important—was not merely the evolution of some new trait. It meant that *the way evolution works* was changed forever. Or as Calcott and Sterelny put it, "Like a robot that continually reprograms itself, or a factory that manufactures parts to change its own operation, evolution upgrades itself, amplifying the kinds of further change that are possible" (p 4).

Scientists sometimes find it helpful to think of evolutionary history as a pathway that a lineage takes through a multidimensional morphospace—a "space" of possible biological forms. Maynard Smith and Szathmáry's work provoked biologists to think of that space as something that itself is capable of changing over time. Perhaps new realms of biological possibility open up when a major transition occurs. Many of the major transitions, such as the evolution of eukaryotic cells, also seem to involve boosts of biological complexity. Studying these major transitions is thus one way of approaching the evolution of complexity.

Calcott and Sterelny's volume is the product of a workshop sponsored by the Konrad Lorenz Institute for Evolution and Cognition Research (KLI) at the University of Vienna. The contributors include a mix of scientists and philosophers of biology. The quality of the papers is very high, and even those who are already familiar with the issues will learn a great deal from them. The first of the three sections ("A big picture of big pictures of life's history") is largely philosophical, while the second ("The prokaryote's tale") focuses more on microbiology. The third section ("Complexity and the developmental cycle") contains mostly scientific papers that engage with questions about multicellular life. The volume concludes with a short, forward-looking essay by Eörs Szathmáry and Chrisantha Fernando. Oddly, this concluding piece focuses not on the history of life but on evolutionary processes that take place during the development of the nervous system, and whether those processes involve any major transitions.

Be forewarned that this is not an introductory book. Although the introduction by Calcott and Sterelny is accessibly written, as are their introductions to the three sections, most of the contributions presuppose some familiarity with recent work in evolutionary biology and its philosophy. And many of the individual papers are quite demanding. Nevertheless,

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this collection provides an excellent snapshot of some of the work that Maynard Smith and Szathmáry have inspired. The papers collected here do reward careful study.

In a paper published in *Nature* around the same time as their book, Maynard Smith and Szathmáry (1995b:228) identified the following transitions as the "major" ones:

Replicating molecules to populations of molecules in compartments

Unlinked replicators to chromosomes

RNA as gene and enzyme to DNA and protein (genetic code)

Prokaryotes to eukaryotes

Asexual clones to sexual populations

Protists to animals, plants, and fungi (cell differentiation)

Solitary individuals to colonies (non-reproductive castes)

Primate societies to human societies (language)

Once you start looking at evolutionary history with these major transitions in mind, you encounter a number of challenging empirical and theoretical questions. For example, what caused some of the particular transitions listed above, and how can scientists study those causes empirically, given that most of the major transitions occurred in the distant past? And how might the study of these major transitions intersect with multilevel selection theory? Are there any transitions that should be on this list but aren't? Are there any that don't belong here?

The paper by Daniel McShea and Carl Simpson ("The miscellaneous transitions in evolution") is the only one that openly challenges Maynard Smith and Szathmáry's program. McShea and Simpson argue that the idea of major transitions lacks theoretical unity. Actually, they have some harsher words than that: according to them, there is "something philosophically muddled and scientifically casual" about it (p 32). Their main complaint is that the list of major transitions is a heterogeneous grab bag, and they direct their fire at the idea that the evolution of human societies from primate societies deserves to be considered a distinct transition. Maynard Smith and Szathmáry most likely included it on their list because the evolution of language involves a change in the way information is stored and transmitted—that's one of the three marks of a major transition that they offer in their 1995 paper. Human societies also involve division of labor, which is the second of the three marks. But the third one is this: "Entities that were capable of independent replication before the transition can only replicate as parts of a larger unit after it" (1995b:227). This doesn't seem to apply to human societies. It doesn't seem to apply to the evolution of sex, either (though see Richard Michod's contribution to this volume for a different perspective).

As if to confirm McShea and Simpson's suspicions about the lack of theoretical unity, two (very interesting) papers in this volume—by Lindell Bromham and by Andrew Knoll and David Hewitt—focus on the Cambrian explosion, which was not one of Maynard Smith and Szathmáry's original major transitions at all. In their introduction, Calcott and Sterelny argue that the Cambrian explosion deserves to be added to the list (p 11–12).

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McShea and Simpson, are, I think, correct to worry that there is some fuzziness about what counts as a major transition, and why. But then again, it's not entirely clear why we really need a unified theory of the major transitions. Perhaps one conclusion to be drawn from this book is that even without such a unified theory, Maynard Smith and Szathmáry's idea has inspired some fruitful scientific and philosophical work. Calcott and Sterelny's collection should inspire some more.

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