



## The proper place of hopeful monsters in evolutionary biology

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### Abstract

Hopeful monsters are organisms with a profound mutant phenotype that have the potential to establish a new evolutionary lineage. The Synthetic Theory of evolutionary biology has rejected the evolutionary relevance of hopeful monsters, but could not fully explain the mechanism and mode of macroevolution. On the other hand, several lines of evidence suggest that hopeful monsters played an important role during the origin of key innovations and novel body plans by saltational rather than gradual evolution. Homeotic mutants are identified as an especially promising class of hopeful monsters. Examples for animal and plant lineages that may have originated as hopeful monsters are given. Nevertheless, a brief review of the history of the concept of hopeful monsters reveals that it needs refinements and empirical tests if it is to be a useful addition to evolutionary biology. While evolutionary biology is traditionally zoocentric, hopeful monsters might be more relevant for plant than for animal evolution. Even though during recent years developmental genetics has provided detailed knowledge about how hopeful monsters can originate in the first place, we know almost nothing about their performance in natural populations and thus the ultimate difference between hopeful and hopeless. Studying the fitness of candidate hopeful monsters (suitable mutants with profound phenotype) in natural habitats thus remains a considerable challenge for the future.

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## Introduction: navigating evolutionary biology through the Skylla of gradualism and the Charybdis of intelligent design

Our planet is inhabited by an impressive number of incredibly complex and diverse organisms, such as plants and animals (including human beings). Compared to the complexity of, say, the human body, even the Space Shuttle looks quite poor, and the diversity of insects alone is just breathtaking. Explaining exactly how the great complexity and diversity of life on earth originated is still an enormous scientific challenge (Carroll, 2001). It may first appear unnecessary to point out that the scientific method has to be brought to bear on the problem. In addition to the inherent biological complexity of the problem, however, I currently see two other major obstacles for future progress from a heuristic perspective that may justify such a remark:

- (i) There is the widespread attitude in the scientific community that, despite some problems in detail, textbook accounts on evolution have essentially solved the problem already. In my view, this is not quite correct.
- (ii) There is the opposite view gaining ground mainly outside of scientific circles that living organisms are so complex that they must have been created by an external intelligence – a novel version of creationism known as “Intelligent Design” (ID). A philosophical analysis of whether ID is a scientific hypothesis at all is beyond the scope of this review. In any case, its ability to develop fruitful research programs has remained negligible so far (Raff, 2005). With few exceptions (e.g., see Lönnig, 2004, and references cited therein) biologists do not consider ID helpful in our endeavour to explain life’s complexity and diversity.

This does not mean, however, that we already have a complete and satisfactory theory which explains how the complexity and diversity of life originated. Thus the rejection of ID or other varieties of creationism is not based on the comprehensive explanatory power of any existing evolutionary theory, but has to be considered as an epistemological presupposition and heuristic basis of biology as a natural science. Since we do not have a complete account of the origin of complex organismal features, clarifying their origin arguably remains one of the greatest challenges of biology (Lenski et al., 2003).

All well-supported scientific theories used to explain the complexity and diversity of living beings are variants of evolutionary hypotheses. According to Darwin (1859), evolution is a two-stage process: heritable random variation provides the raw material, natural selection acts as the directing force that leads to the adaptation of organisms to the environment. By uniting the classical observations of morphology, systematics, biogeography and embryology with population genetics the “Synthetic Theory” (or “Modern Synthesis”) of evolutionary biology was developed during the 1930s and 1940s (Dobzhansky, 1937; Mayr, 1942; Simpson, 1944; Mayr and Provine, 1980; Reif et al., 2000; Junker and Hoßfeld, 2001; Junker, 2004). The Synthetic Theory considers evolution usually as the result of changes in allele frequency due to

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