ABSTRACT

Evolvability: a Formal Approach
D.Phil, Trinity 2009
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This dissertation clarifies the concept of evolvability, the increased capacity of some organisms or systems to support evolution, especially the evolution of life-like complexity. I survey the literature, which is spread over the fields of population genetics, developmental biology, artificial life, and microbial and molecular evolution. Finding that researchers have often used the term vaguely and incompatibly I identify five distinct kinds or senses of evolvability. I also identify five key constituent ideas, which I discuss in the context of *organismic evolvability*, a sense of evolvability with deep roots in the traditional fields of animal development and macroevolution. In these fields research into evolvability has historically been hampered by an insufficiently detailed knowledge of development. Research in molecular evolution has produced a thorough knowledge of the folding of RNA into secondary structure, which can be regarded as model of development. This has motivated new approaches to evolvability based on representing development via a single genotype-phenotype mapping function. I build on these approaches to invent new mathematical methods to formalise the traditional ideas. I create an exact model illustrating a classic example of evolvability, the capacity for repeated segmentation and simple modularity. I analyse this with two new formal approaches. First is the *genospace algebra*, a propositional calculus based on graph theory. It is a formal language for describing genotype-phenotype maps. It provides a system for making calculations, proofs, and diagrams about mutational structures in genotype space, and it is flexible enough to allow description at arbitrary degrees of resolution. Second is a pair of concepts, the *genetic leverage* and the *genetic fulcrum*. The leverage provides a crude numerical measure of evolvability, and the fulcrum provides a heuristic for identifying the genomic and developmental causes of evolvability. Besides its specific relevance to diversification and development, evolvability is also crucial to the fundamental question of how evolution produces ordinary biological life. Simulation systems that implement only a conventional textbook model of evolution – systems possessing only variation, inheritance, and selection – fail to evolve anything resembling the complexity of the biological world. Research into evolvability is our best bet to illuminate the "missing ingredient" for life-like evolution.