
Foreword

The subject of animal evolution has been explored and discussed for a century and a half. As long ago as the late 19th century, Ernst Haeckel, a renowned evolutionary biologist and supporter of Darwin, drew some beautiful phylogenetic trees depicting the possible course of animal evolution. Haeckel's trees included many of the major animal groups, placed on the tips of gnarled and life-like branches, each drawn complete with bark and twigs. One could be forgiven for thinking that the framework of animal evolution was completed long ago. Such a view would be grossly mistaken. The past two decades in particular have seen a revolution in our understanding of animal evolution, and revisiting this topic in 2009 is very timely. As the contents of this volume will testify, research into animal evolution is currently in its most vibrant phase ever, with novel conclusions being generated at great pace.

It is interesting to contrast the nature of current research, as described here, to the first golden age of animal evolutionary biology, the late 19th and early 20th centuries. Many of the early zoologists, including Kowalevsky, Metchnikoff, van Beneden, Lankester, Sedgwick, Jägersten, Goodrich, and T. H. Huxley were superb anatomists and embryologists, and their work has left us with a wonderful and extensive legacy of descriptive data. While invaluable for understanding animal form and function, however, these data ultimately proved of less use for discerning deep animal relationships, or understanding homologies and evolutionary transformations. Until very recently, textbooks and specialized works alike carried speculative, and often highly imaginative, scenarios of animal evolution, depicting how various body forms could be derived from others. For every question discussed,

however, there were almost as many scenarios proposed as there were scientists considering the question, and as a consequence debate was often heated, personal, and inconclusive. A comment made by the Rev. T. R. R. Stebbing at the end of a 1910 symposium discussing the origin of vertebrates reveals the lack of progress on just one of these issues: 'When we return home and our friends gleefully enquire, "What then has been decided as to the Origin of Vertebrates?", so far we seem to have no reply ready, except that the disputants agreed on one single point, namely that their opponents were all in the wrong' [Stebbing, T.R.R. (1910) Discussion on the origin of vertebrates. *Proceedings of the Linnean Society of London* **122**, 9–50].

The fundamental problem plaguing the study of animal evolution a century ago was that there was no reliable way to test alternative scenarios, no objective source of data to evaluate putative homologies or proposed relationships. Every scenario was consistent with the available data, although certainly some theories were more outlandish than others! This was the major stumbling block to advance in the study of animal evolution, and it persisted through much of the 20th century. The problem is now clearly in focus and at least part of the solution is at hand. A major component of the solution is based on the application of molecular biology to animal evolutionary biology, in partnership with other approaches including developmental biology and palaeontology. Of course, genetics was first incorporated into evolutionary thinking in the 1920s to 1940s, when the work of Thomas Hunt Morgan, R. A. Fisher, Theodosius Dobzhansky, J. B. S. Haldane, Sewall Wright, Julian Huxley, Ernst Mayr, G. G. Simpson, and G. Ledyard Stebbins gradually merged Mendelian

genetics with Darwinian evolution in a population context, and convincingly explained microevolution through changes in allele frequencies. But it still remained unclear if large anatomical differences, such as those between animal phyla, could be explained in the same way. Even if they could, as many argued, these early genetic studies did not reveal what genes were actually involved, what anatomical transformations had happened in evolution, and hence which of the multiple scenarios for animal evolution were correct. Until the 1980s, those working on evolutionary genetics had little interface with whole-organism biology, including embryology and animal diversity. Zoology was a divided field. As Frank R. Lillie, former Director of the Woods Hole Marine Biological Laboratory, commented in 1927: 'There can be no doubt, I think, that the majority of geneticists, and many physiologists certainly, hope for and expect a reunion. The spectacle of the biological sciences divided permanently into two camps is evidently for them too serious a one to be regarded with satisfaction' [Lillie, F.R. (1927) The gene and the ontogenetic process. *Science* 66, 361].

Lillie's hoped for reunion is now upon us. In the past two decades, molecular genetics has started to have major impacts on the study of animal evolution, and in two distinct ways. First, comparison of DNA sequences is being used to trace evolutionary relationships between long-divergent animal phyla, and thus to reconstruct a fairly true genealogy of animal life spanning over half a billion years. It is not a simple exercise, and one that is fraught with methodological and analytical problems, but enormous progress is being made. It is now clear that combining data from many genes simultaneously, sometimes over 100 different genes from each species, can increase the reliability of phylogenetic inference, as can analysis of rare genome-level changes, such as inversions and rearrangements of the DNA. Examples of both approaches are discussed in this volume. These strategies have greatly benefited from recent advances in high-throughput DNA sequencing, a technology that is moving forward apace, and as such we are truly in the middle of a revolution in animal phylogenetics. Haeckel's trees are being updated with confidence.

The second application of molecular biology is closely linked with comparative embryology, the favoured approach of a century ago. Work on convenient laboratory species, such as *Drosophila*, nematodes, and mice, has produced a wealth of data on the identity and function of genes controlling specific aspects of embryonic development, from setting up of embryonic axes (dorsoventral, left-right, anteroposterior), to the establishment of tissue layers, the formation of organs, and the differentiation of specific cell types. With the discovery that many (but certainly not all) of these genes are ancient and present in highly divergent phyla, it has now become possible to trace how developmental pathways have changed in evolution, or been deployed in different ways, and relate this to the evolution of specific structures in animals. As above, there are technological difficulties and analytical pitfalls, but the results can be highly persuasive. Examples in this volume include new insights into the diversification of nervous systems, evolution of larval forms, relationships between body axes, evolution of segmentation, and the origin of novel characters.

These applications of molecular biology to zoology may have stimulated the reunion of developmental and evolutionary zoology, but they are not taking place in isolation. A holistic understanding of animal evolution is promised as insights from these methods are coupled with deeper knowledge of animal anatomy and embryology, based on old and new data, insights into divergence dates and extinct character combinations, informed through palaeontology, and refined understanding of gene functions. A revolution in understanding animal evolution is upon us.

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