JOHN TYLER BONNER

Foreword

There has been a remarkable explosion of interest in evolutionary developmental biology in the last twenty years and one might well ask why this has occurred. The subject, after all, in a different guise was central to biology in the nineteenth century; it was a subject of importance to Charles Darwin, August Weismann, Ernst Haeckel, and many others, but to some degree it faded in the twentieth century. Embryology concerned itself primarily with the mechanism of development, a subject that goes back to Wilhelm Roux, Hans Driesch, and others; the study of evolution rather aggressively stepped to one side of development as though to keep itself uncontaminated by secondary details.

There were notable exceptions of individuals who brought development and evolution together during the last century, but their ideas never became the popular central issue of either developmental biology or evolution. To name a few who made significant contributions, in the beginning of the century Walter Garstang pushed the idea that it was not just adult animals that evolved; the larval stages of metamorphosing animals also could be independently modified by natural selection. He was followed by Gavin de Beer, who made a spirited effort to expose what he felt was the oversimplification of the problem by the great nineteenth-century propagandist Ernst Haeckel with his biogenetic law that ontogeny recapitulates phylogeny. The subject was far richer than that and de Beer did a fine job of exploiting that richness, although he did it by coining a large number of forgettable terms.

By the mid-twentieth century, we began to hear new thoughts on the subject from Ivan Schmaulhausen and Conrad Waddington. The latter's work is particularly interesting because he made a concerted effort to bring genetics and development together and thought of them in an evolutionary context. He felt quite strongly that the new synthesis of evolutionary biology—population genetics—seriously missed the mark. It was a hollow quest because it completely ignored how genes are involved in the formation of the adult: what genes do is direct development, and that is what evolves. From today's perspective he was certainly on the right track, though his ideas, while greatly admired by many, had only a modest impact.

In the 1950s and 1960s, as the popularity and importance of biochemistry increased, scientists began to examine the nature of the chemical messengers that account for the many events of development. In particular they wanted to know the nature of the substances that emanated from the dorsal lip of the blastopore that induced the amphibian embryo to form. This was the key to understanding embryonic induction, discovered in the 1920s by Hans Spemann and Hilda Mangold in their famous experiment showing the remarkable stimulating properties of this region, which they called the "organizer." The problem seemed manageable until Johannes Holtfreter discovered that implanted dead organizer tissue could also induce a secondary embryo, thereby showing that the region might be giving off chemical stimuli. This led a number of researchers to try to isolate and characterize those chemicals. The search was not successful and while "chemical embryology" in other forms was central for a while, it was an area of research of modest success.

The crucial change came with the advent of molecular genetics: suddenly there was a new way of examining the causes of development—the main object of experimental embryology for the previous one hundred years. Ultimately the chemical nature of the induction described by Spemann and Mangold and various other mysteries were solved, or are within reach of being solved. The key genes involved in pattern and many other processes in development could now be identified along with the proteins they specified; the chemical details of causal embryology could be explored at a far deeper level. One of the great outcomes of this new plan of study was the discovery that these genes existed in widely different groups of organisms, sometimes with the same function, sometimes with a different one. In this way, in a brilliant flash, development again hooked up with evolution. We could examine the evolution of development in a new and exciting way.

It is striking that the big jumps forward in the twentieth century all involved the coming together of two disciplines, and in each of these momentous collisions, genetics was one of the components. The first occurred in the 1900s when Mendel's genetics encountered chromosomal cytology and cytogenetics was born. In the 1930s genetics collided with evolution to produce population genetics, which had, and continues to have, a significant impact on our thinking. The greatest explosion of all was when genetics collided with biochemistry in the 1950s to produce molecular biology. Finally, in the 1980s genetics—now molecular genetics—quite accidentally produced wonders by joining with evolution to produce modern evolutionary developmental biology. This most recent wave not only has shown great promise for the future, but has its roots far back in the nineteenth century.

With the new interest in the marriage of evolution and development, nothing could be more timely and appropriate than this compendium of keywords and concepts. Over the last two centuries, words and ideas have continued to emerge. For Darwin, evolution and development were closely intertwined; now they have come together again in an important and integrated way.