

## Foreword

David Botstein

Science is both a rational and a social endeavor. The basic paradigm for scientific progress, comprising a progression from observation to theory and experimentation, has been in place for several hundred years. Mostly science moves in steps small enough so that the introduction of a new idea, theory, or point of view is followed fairly quickly by a consensus among scientists who become convinced by the evidence. Scientists are taught to value new ideas and to evaluate the evidence, even when new ideas are revolutionary and fundamental. Often they have no difficulty doing so: Einstein's astonishingly original ideas were understood and largely accepted by physical scientists within a decade or so of their publication.

Occasionally, however, there are geniuses who make observations, propose theories, and carry out convincing experiments that are somehow so far in advance of contemporary scientific understanding that the general acceptance of their ideas, even by the scientific community, lags for many decades. The work of three well-known giants in the history of biology displayed this kind of intellectual "prematurity": Charles Darwin, Gregor Mendel, and Barbara McClintock.

This book is a compendium of what is known and accepted today about transposons and genomic dynamics in plants, a field whose basic ideas manifestly derive from the work and insights of Barbara McClintock to a degree similar to the influence of Mendel on genetics and Darwin on evolution. As with Darwin and Mendel, acceptance of McClintock's ideas has taken many decades. But unlike Darwin and Mendel, the depth of her insight is still to be fully appreciated.

What stood in the way? Some of McClintock's discoveries, such as the relationship between chromosomes and linkage groups, achieved immediate acceptance. Transposition, by contrast, took decades and repeated rediscovery in organisms other than maize. Still others, such as the concept that genomes sense and respond to external stimuli, are just beginning to find experimental support and intellectual acceptance.

The barrier was not obscurity or even gender. McClintock achieved a high status early in her career on the basis of her achievements. Unlike Mendel, she and her ideas were well known and widely accepted in her community. Despite her eminence, other scientists appear simply to have failed to understand some of her ideas or the evidence on which they were based. Unlike the case of Darwin, there were no religious or ideological barriers to the acceptance of McClintock's ideas. Hers seems to have been purely a matter of having been ahead of her time.

But I also believe that two commonly held convictions had to change to make way for full acceptance of McClintock's ideas about genome dynamics in evolution, which are the subject of this book. The first was the generalization that only proteins and their regulation are really important in understanding biology and evolution. The second was the conviction that the mechanisms of evolution could not themselves evolve.

The focus on proteins was entirely understandable: it was at the heart of the molecular biology revolution. Molecular biologists explicitly taught the “central dogma” that information flows from DNA to RNA to protein and only thence to phenotype and fitness. No surprise, then, that the biological community sought to understand everything in terms of proteins and their regulation. This led to an unwanted and, and surely unintended consequence: dismissal of noncoding DNA as “junk.” Of course, this “junk” included all the transposons and transposon remnants that, as readers of this book will see, are what make the genome dynamic and are the drivers of genome evolution.

The misunderstanding about evolution of evolutionary mechanisms arose from the long-running debate about Darwinism, not only among scientists, but also in society more generally. Countering religious rejection of Darwinism in favor of divine intention and teleological arguments, scientists rather vehemently rejected the legitimacy of teleology in scientific reasoning. This rejection led, perhaps unwittingly, to the dismissal of “evolvability” as a property that could be selected in evolution. For most of the twentieth century, the scientific community treated the concept of evolvability as requiring something like intention or, at least, precognition.

The idea that one genome is more fit than another because it is more mutable was an idea that, at best, was hard to imagine. The dismissal of transposons as “junk” DNA and as “parasites” whose destructiveness genomes must rigidly control also interfered with perception of their contribution to evolvability. Thus in order for McClintock’s ideas about genome dynamism to be accepted, it was first necessary for the scientific community to assimilate the existence and sheer genomic abundance of transposons and then to appreciate their agency in the mechanisms of chromosome mechanics and functional evolution.

This book is a thorough examination of the current state of knowledge about the numbers and nature of transposons and retrotransposons and how they have shaped plant genomes. Progress of this more incremental variety has come through the invention and application of rapid techniques for genome and transcript analysis. The results have led to a renewed appreciation that Barbara McClintock understood much more than the basic ideas of chromosome mechanics and transposition, both of which were already widely accepted by the time of her death in 1992.

Indeed, McClintock discovered and recognized the significance of what we now call “epigenetics” – the heritable, reversible regulation of gene activity. The study of epigenetics and epigenomics has only recently become one of the hottest research fields of our time. The larger community is just now beginning to assimilate fully the notion that phenotypes reflect not only genotypes but also the epigenetic consequences of both development and response to the environment. Finally, and perhaps most importantly, McClintock understood, as the rest of us are only beginning to figure out, that there are well-orchestrated genomic stress responses that can rapidly restructure genomes – the quintessence of evolvability.