PREFACE

The nature of heredity—that is, how biological information is transmitted across generations—is a question that touches just about every part of the biomedical sciences, from evolutionary biology's quest to account for the diversity of life to medical science's effort to understand why certain diseases run in families. It's also widely seen as an iconic success story of modern science. From the cautious speculations of the nineteenth century to the establishment of Mendelian genetics in the early twentieth century and the deciphering of the genetic code in the 1960s, the unlocking of "the mechanism of heredity" is portrayed in textbooks as a journey now essentially completed.

But nature often manages to frustrate our desire for simple answers. Several decades of troubling discoveries that don't fit the established picture of how the world is supposed to work are now leading some scientists to argue that it's time to rethink the nature of heredity. If this challenge succeeds, then the biological and medical sciences will be in for a shake-up over the coming years, and even the textbooks will have to be rewritten.

If we were to try to summarize the main thesis of this book in a few words it would be like this: there is more to heredity than DNA sequences (genes), and recognizing this nongenetic dimension of heredity can provide us with new insights into how evolution works, and into many practical concerns of human life as well. It's now clear that a variety of nongenetic factors are transmitted across generations alongside genes. Like genes, such nongenetic factors can convey biological information across generations, confer a resemblance between offspring and their parents, and potentially influence the course of evolution. This

plurality of hereditary factors is necessitated by basic properties shared by all cellular life-forms, and we believe that any concept of heredity that is not arbitrarily narrow must encompass this nongenetic dimension. A concept of heredity that encompasses both genetic and nongenetic processes is already emerging, and we will refer to it as "extended heredity" to differentiate it from the conventional, genocentric view.[1]

The narrow concept of heredity that has prevailed since the early decades of the twentieth century has resulted in the exclusion from the realm of possibility of some very real and important biological phenomena, such as the possibility that an individual's experiences during its lifetime can have predictable consequences for the features of its descendants. Such effects were long dismissed as a "chemical impossibility" and a violation of the "central dogma" of molecular biology. Yet, a great variety of such phenomena have now been reported in the scientific literature. This nongenetic side of heredity has been a blind spot for biology and medicine for decades, but the elephant in the room is finally starting to be noticed. For readers who are new to this field, we aim to provide a way to think about these recent developments, place them in historical context, and understand their implications. For those who remain skeptical of such heterodox ideas, we hope to at least bring the issues into sharper focus.

We are not the first to recognize the implications of nongenetic inheritance. In this book, we draw on numerous lines of research by many authors, borrowing from such far-flung areas as cultural inheritance theory, niche construction theory, evolutionary ecology, and molecular and cell biology. Work in all these areas has addressed various aspects of what the classic narrative leaves out.[2] Most importantly, two thought-provoking books by Eva Jablonka and Marion Lamb—*Epigenetic Inheritance and Evolution* (1995) and *Evolution in Four Dimensions* (2005)—have focused squarely on the implications of nongenetic inheritance for evolution. Jablonka and Lamb's books and papers paved the way for the recent upsurge in evolutionary research on extended heredity, and crystallized many of the ideas explored by subsequent authors, including ourselves. Yet, while we acknowledge our intellectual debt to Jablonka and Lamb, this book reflects our own perspective, approach, and aims. In particular, building on the conceptual groundwork laid by previous authors, our main objective is to explore how an extended concept of

heredity can be incorporated into evolutionary theory and why doing so can provide new insight on a range of evolutionary questions.

We have subdivided this book into ten chapters.

In chapters 1 ("How to Construct an Organism") and 2 ("Heredity from First Principles"), we explain why the classic framework is overly narrow, and why we believe that an extended concept of heredity is necessitated by universal features of cellular life. These chapters introduce ideas that are developed more fully in the rest of the book.

In chapter 3 ("The Triumph of the Gene"), we explore the development of the modern, genocentric concept of heredity. Although scientists rarely bother to delve into the historical baggage of their discipline, we believe that without understanding the history it is all but impossible to understand current developments in this field. For example, why is it that nongenetic inheritance was so unequivocally rejected by leading twentieth-century biologists? And why are their arguments no longer valid today?

Chapters 4 and 5 provide an overview of the evidence for nongenetic inheritance and illustrate its diversity and importance. Chapter 4 ("Monsters, Worms, and Rats") focuses on fascinating discoveries of a type of nongenetic inheritance, known as "epigenetic inheritance," that has recently been receiving a lot of attention in medical science as well as the mainstream media. In chapter 5 ("The Nongenetic Inheritance Spectrum"), we show that phenomena that are "epigenetic" in the strict sense are part of a much broader array of nongenetic inheritance mechanisms that are just as interesting and important.

The next set of chapters explores the implications of extended heredity in more depth. In chapter 6 ("Evolution with Extended Heredity"), we show how the ideas developed in earlier chapters can be incorporated into evolutionary theory, furnishing a framework that allows us to explore their consequences for evolution. In chapter 7 ("Why Extended Heredity Matters"), we use this framework to illustrate how nongenetic inheritance can change the trajectory and outcome of evolution. In chapter 8 ("Apples and Oranges?"), we confront the key criticisms that evolutionary biologists have leveled against extended heredity. In chapter 9 ("A New Perspective on Old Questions"), we revisit some of the thorniest puzzles in evolutionary biology and show how the insights provided by extended heredity can allow us to see these questions in a new light.

Finally, in chapter 10 ("Extended Heredity in Human Life"), we consider the implications of extended heredity for the practical concerns of modern human beings living in a rapidly changing world. We show that, during its heyday in the twentieth century, the narrow, genocentric view of heredity had very tangible and sometimes tragic consequences, and we consider how extended heredity might alter our understanding of our health and society, and our impact on the world around us.

We have endeavored to make this book as accessible as possible in the hope that it will be read not only by practicing biologists but also by students and laypeople who follow biology. While jargon is sometimes unavoidable, we have made an effort to define all technical terms (with some definitions and explanations provided in notes at the back of the book). Where mathematical ideas form an essential part of the story, we have tried to present them in intuitive and pictorial ways. Equations have been kept to a minimum and are mostly consigned to boxes and notes that lay readers can safely skip without losing the bigger plot.

We devote relatively little space to discussion of molecular mechanisms. Our main aim in this book is to explore the implications of extended heredity for evolution and, for this reason, we focus on effects at whole-organism and ecological levels and provide just enough detail on proximate mechanism to allow readers to understand the general nature of these effects. Moreover, molecular biology is developing at such a breathtaking pace that any details we provide are likely to be outdated by the time this book rolls off the printing press. Readers who wish to delve deeper into the details of molecular mechanism can easily find up-to-date reviews.

We should also state at the outset that the ideas presented in this book do not refute evolutionary theory or the central role that genetics plays in it. We see genetic and nongenetic inheritance as hereditary processes that operate in parallel, so extended heredity supplements rather than supplants genetics. Likewise, although we believe that these ideas have important implications for evolutionary biology, extended heredity does not challenge Darwin's basic insight that natural selection coupled with inheritance is the primary cause of adaptive evolution.

Who are we? RB is an evolutionary biologist in the Evolution and Ecology Research Centre and School of Biological, Earth, and Environmental Sciences at the University of New South Wales in Sydney,

Australia. TD is cross-appointed between the Departments of Biology and Mathematics at Queen's University in Kingston, Canada. Since meeting at the University of Toronto around the turn of the century, we have collaborated on a number of research projects and, somewhere along the way, became interested in extended heredity and its implications for evolution. This book is the culmination of several years of collaborative research on this problem.