

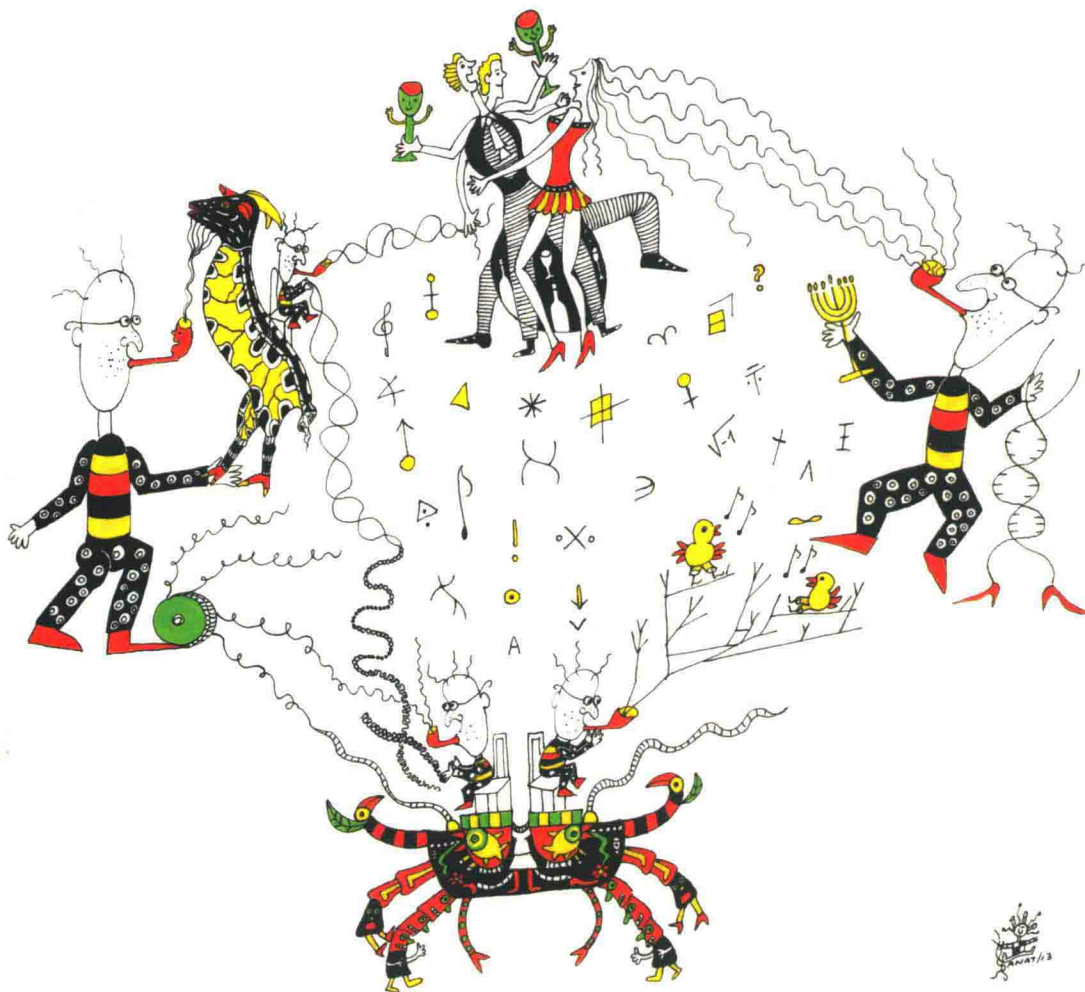
Evolution in Four Dimensions

Genetic, Epigenetic, Behavioral, and
Symbolic Variation in the History of Life

va Jablonka and Marion J. Lamb

ustrated by Anna Żeligowski

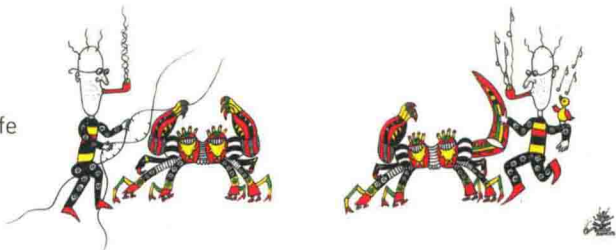
revised edition



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This new edition of the widely read *Evolution in Four Dimensions* has been revised to reflect the spate of new discoveries in biology since the book was first published in 2005, offering corrections, an updated bibliography, and a substantial new chapter. Eva Jablonka and Marion Lamb's pioneering argument proposes that there is more to heredity than genes. They describe four "dimensions" in heredity—four inheritance systems that play a role in evolution: genetic, epigenetic (or non-DNA cellular transmission of traits), behavioral, and symbolic (transmission through language and other forms of symbolic communication). These systems, they argue, can all provide variations on which natural selection can act.

Jablonka and Lamb present a richer, more complex view of evolution than that offered by the gene-based Modern Synthesis, arguing that induced and acquired changes also play a role. Their lucid and accessible text is accompanied by artist-physician Anna Zeligowski's lively drawings, which humorously and effectively illustrate the authors' points. Each chapter ends with a dialogue in which the authors refine their arguments against the vigorous skepticism of the fictional "I.M." (for Ipcha Mistabra—Aramaic for "the opposite conjecture"). The extensive new chapter, presented engagingly as a dialogue with I.M., updates the information on each of the four dimensions—with special attention to the epigenetic, where there has been an explosion of new research.

Eva Jablonka is Professor at the Cohn Institute for the History and Philosophy of Science and Ideas at Tel Aviv University. Marion J. Lamb was Senior Lecturer at Birkbeck College, University of London, before her retirement. Jablonka and Lamb are also the authors of *Epigenetic Inheritance and Evolution*.

Life and Mind series
A Bradford Book

Praise for the first edition

"In their beautifully written and impressively argued new book, Jablonka and Lamb show that the evidence from more than fifty years of molecular, behavioral and linguistic studies forces us to reevaluate our inherited understanding of evolution."

—Oren Harman, *The New Republic*

"It is not only an enjoyable read, replete with ideas and facts of interest but it does the most valuable thing a book can do—it makes you think and reexamine your premises and long-held conclusions."

—Adam Wilkins, *BioEssays*

Cover illustrations by Anna Zeligowski

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Revised Edition

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with illustrations by Anna Zeligowski



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Evolution in Four Dimensions

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To our genetic, epigenetic, and cultural parents and offspring

Preface to the Revised Edition

Since *Evolution in Four Dimensions* was first published, there has been a spate of new and exciting discoveries in biology. Many of the new findings are directly relevant to the topics we discussed in 2005, by and large supporting and often strengthening the arguments we put forward then. In addition to new facts, new ideas about evolution have also emerged; biologists have been questioning the assumptions on which twentieth-century evolutionary theory was based, and have proposed alternative ways of approaching evolutionary problems. In this edition of *E4D*, we introduce some of the new knowledge and fresh ideas, in the firm belief that they add weight to our view that the old, gene-based, Modern Synthesis version of evolutionary theory is inadequate for the twenty-first century.

We have left parts I to III of the book almost unchanged from the original edition, making only a few minor corrections, mainly typographical. For the benefit of ebook readers, we have also numbered all the endnotes chapter by chapter, and included markers for them in the text. Most of the new material is to be found in part IV, which is a single, long, additional chapter. To carry the reader through this we have made use of the dialogue form employed elsewhere in the book, with our interrogator (IM) asking us (ME) questions and questioning the answers we give. The chapter has five sections; in the first four, we go through each of our dimensions—the genetic, the epigenetic, the behavioral, and the symbolic—reviewing and updating the ideas and facts presented earlier. We devote quite a lot of space to the involvement of epigenetics in the other dimensions of heredity, because there has been an explosion of information in this area, which is both empirically and conceptually groundbreaking for evolutionary theory. In the fifth section of the chapter, we look at the general implications of the work we have been describing for ideas about evolution.

At the beginning of the endnotes for each chapter, we have added a short “nine years later” paragraph, in which we signpost where in the literature recent information is to be found. Many references have been added to the reference list, and there are additional entries in the index. With the help of Anna Zeligowski’s drawings, we have tried to present the new material in a way that retains the spirit of the original edition of *E4D* and enhances its usefulness.

Acknowledgments

This book would not have been written without the encouragement and help of our friends, families, students and colleagues. We are grateful to all of them.

Part of the book was written while E. J. was a visitor at the Museum of Vertebrate Zoology, Berkeley, University of California, and we would like to thank David and Marvalee Wake and their colleagues for the good working environment they provided, and Martha Breed and the WW group for their company and the wonderful nature trips. We also want to thank everyone working at the Cohn Institute for the History and Philosophy of Science and Ideas at Tel Aviv University for their help and support. Our debt to the students in the Cohn Institute and the participants in the "Networks in Evolution" seminar at the European Forum Alpbach 2002 is a big one. Their comments and criticisms made us clarify many of our ideas and arguments, abandon some of them, and think deeply about how we should present the material in this book. We hope that they will enjoy the final product.

We have benefited from information and advice from many people, but our special thanks must go to those who have read and commented on various drafts of the book. Eytan Avital, Daniel Dor, Fanny Doljanski, Yehuda Elkana, Yehudit Elkana, Evelyn Fox Keller, James Griesemer, Revital Katznelson, Jawed Iqbal, Lia Nirgad, Christine Queitsch, Richard Strohman, Iddo Tavory, and Alan Templeton each read sections or chapters, and pointed out some of the errors and ambiguities in what we had written. Our long-suffering friends Lia Ettinger, Simona Ginsburg, and Joy Hoffman read drafts of the whole book, and their comments, criticism, and many valuable suggestions have made it a far better book than it would otherwise have been. Tom Stone, Philip Laughlin and their colleagues at the MIT Press were helpful and encouraging throughout, and we thank them for their guidance and excellent editorial work.

We also want to thank Rami of the Ha'Shloshah restaurant in Jerusalem. His hamousta soup sustained us through many long days, and many problems were resolved at his tables.

Finally we need to acknowledge the contribution of Beauty-the-cat, who sat on every page of the manuscript, thereby delaying its completion by several weeks. As an ex-feral cat, she was a constant reminder of the power of learning, active niche construction, and the coevolution of humans and cats.

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Prologue

The content and format of this book are a little unusual, so we want to begin by explaining what it is about and how it is organized. Our basic claim is that biological thinking about heredity and evolution is undergoing a revolutionary change. What is emerging is a new synthesis, which challenges the gene-centered version of neo-Darwinism that has dominated biological thought for the last fifty years.

The conceptual changes that are taking place are based on knowledge from almost all branches of biology, but our focus in this book will be on heredity. We will be arguing that

- there is more to heredity than genes;
- some hereditary variations are nonrandom in origin;
- some acquired information is inherited;
- evolutionary change can result from instruction as well as selection.

These statements may sound heretical to anyone who has been taught the usual version of Darwin's theory of evolution, which is that adaptation occurs through natural selection of chance genetic variations. Nevertheless, they are firmly grounded on new data as well as on new ideas. Molecular biology has shown that many of the old assumptions about the genetic system, which is the basis of present-day neo-Darwinian theory, are incorrect. It has also shown that cells can transmit information to daughter cells through non-DNA (epigenetic) inheritance. This means that all organisms have at least two systems of heredity. In addition, many animals transmit information to others by behavioral means, which gives them a third heredity system. And we humans have a fourth, because symbol-based inheritance, particularly language, plays a substantial role in our evolution. It is therefore quite wrong to think about heredity and evolution solely in terms of the genetic system. Epigenetic, behavioral, and symbolic inheritance also provide variation on which natural selection can act.

When all four inheritance systems and the interactions between them are taken into account, a very different view of Darwinian evolution emerges. It is a view that may relieve the frustration that many people feel with the prevalent gene-centered approach, because it is no longer necessary to attribute the adaptive evolution of every biological structure and activity, including human behavior, to the selection of chance genetic variations that are blind to function. When all types of hereditary variation are considered, it becomes clear that induced and acquired changes also play a role in evolution. By adopting a four-dimensional perspective, it is possible to construct a far richer and more sophisticated theory of evolution, where the gene is not the sole focus of natural selection.

We have divided the book into three parts, each of which has a short introduction. Part I is devoted to the first dimension of heredity and evolution, the genetic system. In chapter 1 we outline the history of Darwin's theory and show how it became so gene-centered. Chapter 2 describes how molecular biology has changed the way biologists see the relation between genes and characters. In chapter 3 we examine the evidence suggesting that not all genetic changes should be seen as random, chance events.

Part II deals with the other dimensions of heredity. Chapter 4 is about the second dimension, epigenetic inheritance, through which different cells with identical DNA are able to transmit their characteristics to daughter cells. In chapter 5 we explore the ways in which animals transmit their behavior and preferences through social learning, which is the third dimension. We deal with the fourth dimension in chapter 6, which describes how information is transmitted through language and other forms of symbolic communication.

In part III of the book we put Humpty Dumpty together again. Having looked at each of the four dimensions of heredity more or less in isolation, we bring them together by showing how, in the long term, the systems of inheritance depend on each other and interact (chapters 7 and 8). In chapter 9 we discuss how they may have originated and how they have guided evolutionary history. Finally, in chapter 10, we summarize our position and put it into a wider perspective by considering some of the philosophical implications of the four-dimensional view, as well as some political and ethical issues.

Each chapter ends with a "dialogue," and the whole of chapter 10 takes this form. We use these dialogues as a device to enable us to reiterate some of the tricky points in our arguments, and to highlight areas of uncertainty and issues that are contentious. The participants in the dialogues are M.E. (who represents the authors, Marion Lamb and Eva Jablonka) and someone