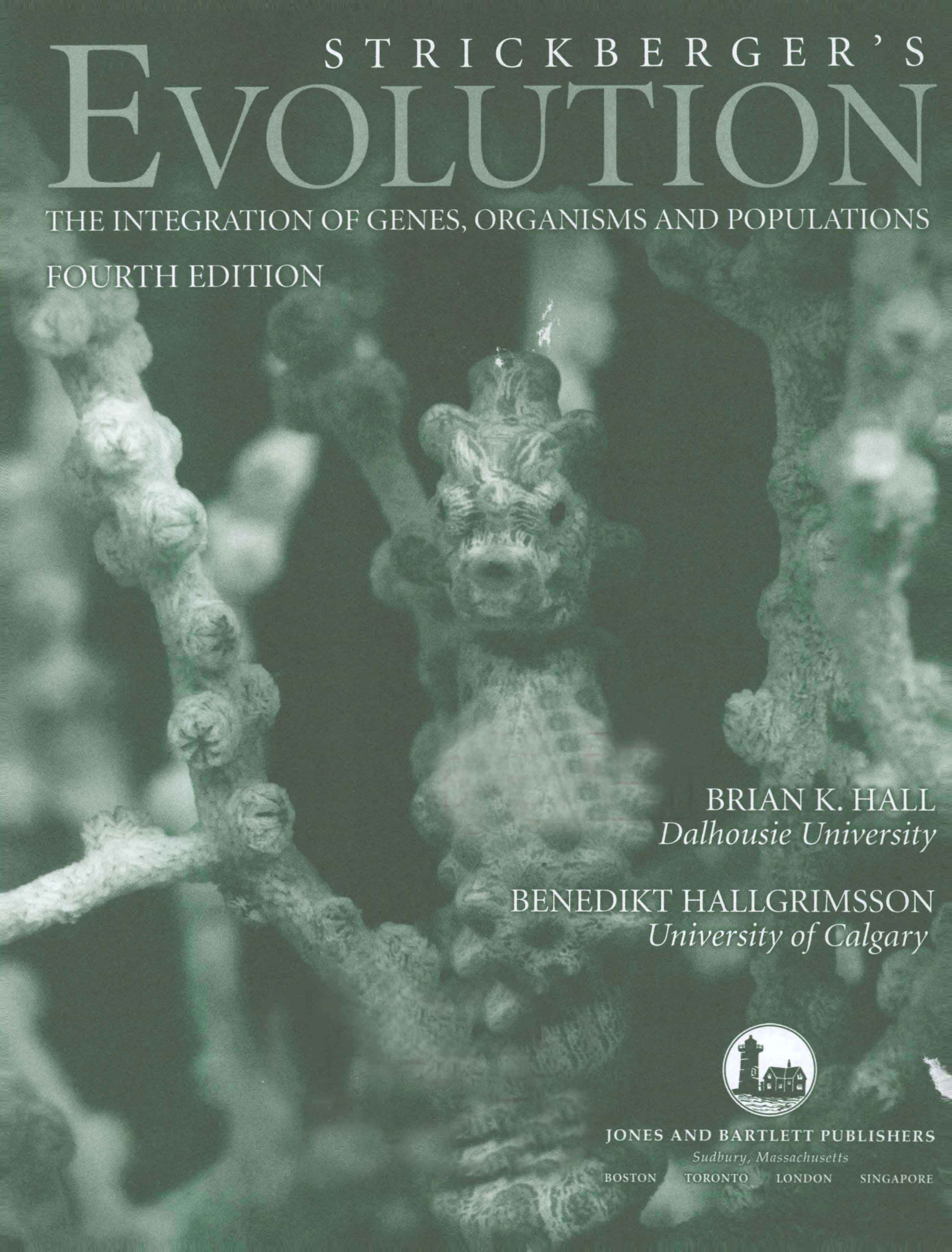
STRICKBERGER'S

EVOLUTION

FOURTH EDITION

BRIAN K. HALL
BENEDIKT HALLGRIMSSON



STRICKBERGER'S EVOLUTION

THE INTEGRATION OF GENES, ORGANISMS AND POPULATIONS

FOURTH EDITION

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The animal pictured in the right-hand page corner throughout this book is an early tetrapod, a "four-footed" animal. Moving from water to land was a critical step in tetrapod evolution; fossil evidence of stem and early tetrapods indicates that this occurred about 365 million years ago (see Chapter 18). Hypothesized advantages to moving to land include avoiding predators and exploiting terrestrial food sources, such as insects. Flip the pages of this book from front to back to watch the animal "evolve."

About the cover: Pygmy seahorse (*Hippocampus bargibanti*) camouflaged on a sea fan coral (Muricella sp.). These seahorses have scaleless bodies and prehensile tails, which they may use to hold on to their gorgonian home. The coloration and texture of this tiny seahorse has evolved to match the color and shape of its host coral. It inhabits the tropical coral reefs of the western Pacific Ocean and reaches no more than 2.4 centimeters in length. Photographed in Pulau Kapalai, Sabah, Malaysia.

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Preface

It has been a privilege to have been given the opportunity to revise and update *Evolution* by Monroe Strickberger, the most broadly based textbook on evolution. Available in three editions, the first in 1990, the third in 2000, *Evolution* has become a staple for undergraduate education in evolutionary biology. Over the last six years, however, the field has changed enormously. A major change is that embryonic development, which separates natural selection from its effect on genes, is no longer a black box; an entirely new field linking evolution with development has come into a mature phase of development. Another is that the sequencing of entire genomes and the emergence of bioinformatic tools for dealing with such vast quantities of information is beginning to allow us to ask questions at the level of biological systems rather than individual genes. Finally, the fossil record continues to expand and our understanding of it continues to mature, especially through paleobiology, the integration of paleontology with such biological disciplines as ecology, developmental biology and physiology. To the best of our ability, the fourth edition incorporates these changes in evolutionary biology and the broader biological sciences.

Essential to our understanding of evolution is that groups of organisms are bound together by their common inheritance; that the past has been long enough for inherited changes to accumulate; and perhaps most essential of all, that discoverable biological processes and natural relationships among organisms explain the reality of evolution. Although each of these aspects has been studied and discussed at various times in human history, only after the mid-nineteenth century when Charles Darwin developed his theory of evolution by natural selection did biological evolution become an acceptable scientific alternative to earlier explanations. This acceptance brought about enormous changes in how we view the world, understand our place in it, and explain natural phenomena.

Of special interest in historical sciences such as evolution is the emphasis on understanding a particular sequence of historical events that cannot always be understood by the application of general laws such as those of physics and chemistry. For example, subjects of historical sciences include events that led to our solar system, to the separation of South America from Africa and to the origin of humans, recognizing at the same time that these events are singular and do not apply to all stars, all continental separations or the evolution of all species. Thus, although sciences that deal with the past make use of general laws such as gravity, mechanics and biochemistry, *their aim is to discover the causes of diversity and uniqueness as much as to discover principles and laws that apply uniformly to all matter or all life.* Indeed, the ability to extrapolate from general principles *and* to explain the role of contingency is both central to the dynamic interdisciplinary nature of the study of evolution and makes it a robust and testable science. The properties of different hydrogen atoms, for example, can be explained on a common physical basis, whereas the properties of different organisms — the organization and function of their component parts — are explained within the context of their organismal histories, which include adaptations to specific lifestyles at particular times. *The central aim of evolutionary biology is to explain the origins and diversity of life.*

When historical conditions are repeated, and different organisms are subjected to similar selective evolutionary forces, some common features can be predicted; geographically widely separated populations and species, such as fish adapted to cave conditions, consistently show rudimentary eyes, enhanced development of chemosensory organs and loss of pigment, among other common attributes. Other evolutionary changes are contingent on past history, for example, the evolution of flight among reptiles and not among frogs or most mammals. In this text we both provide the evidence upon which general principles can be based and explore those aspects of organisms and biological processes involved in historical contingency. To this end, there is a logic in the way we have arranged the subject matter:

- beginning with the history of evolutionary ideas (Part 1);
- moving to the origins of the universe, Earth, molecules, cells, organisms and natural selection in Part 2;
- considering the genetic basis for inheritance, the nature of species, how species are grouped and the role of development in evolution in Part 3; before
- examining the major groups of organisms on Earth (Part 4);
- discussing how populations are maintained and how species arise (Part 5);
- finishing with how cultural, social and biological evolution interact in our own population, how humans have had an impact on the evolution of other species and how evolution has an impact on religion (Part 6).

PART 1 provides the historical, cultural and social framework leading up to Darwin's theory of the origin of species by means of natural selection. We approach the history of evolutionary biology by asking, "What happened?" "Who were the major players?" and "Why did it happen the way it did?"

PART 2 deals with events that occurred between 5 and 15 billion years ago (Bya is the abbreviation we use throughout) to create 100 billion galaxies, each with 100 billion or more stars, of which Earth's is one in a solar system that arose 4.6 Bya. Earth's origin, how molecules arose, whether the first molecules were DNA, RNA or protein, and how the first prokaryotic and eukaryotic cells arose 3.5 Bya and 2 Bya, respectively, are all discussed in the five chapters of Part 2.

PART 3 takes us into the realms of genes, cells and organisms as we consider those fundamental genetic, molecular, cellular and developmental features and processes that provide the basis for inheritance, variation and evolution — *descent with modification,* to use Darwin's terms. Now that we know that much of the genome is shared between organisms and has an evolutionary history that can be traced back to the origins of eukaryotes, much emphasis is being placed on gene regulation as pivotal to developmental and evolutionary change. Change the level or time of expression of a regulatory gene and you can change the phenotype. Selection on that new phenotype can result in the altered state of gene expression spreading through the population, leading to evolutionary change — descent with modification. The five chapters in Part 3 provide the background for you to appreciate how such modification occurs and how we recognize new species when they arise.

PART 4 contains seven chapters on the history of life in which we consider the diversity of organisms that now populate and have populated Earth. Emphasis is on how new groups of organisms arise and adapt to changing environments, and how organisms are related one to another. Much in these seven chapters is about transitions — from unicellular protozoans to multicellular plants and animals; from water to land in plants and animals; from invertebrates to vertebrates; from jawless to jawed vertebrates; from reptiles to birds.

PART 5 examines those genetic and other mechanisms operating to maintain populations as stable entities or to change populations and allow new species to arise.

PART 6 takes us into how cultural and biological evolution interact in our own species, how we now have the ability to influence the evolution of other species and how evolution and religion interact.

Although there is a logical arrangement for Chapters 1 to 26, the structure of the book allows you to begin with Part 6 or to read individual parts as units independent of the other parts.

Summaries are provided at the beginning of each of the six parts and at the beginning of each chapter. We suggest that you read the summary both before and after you read each chapter — before to see whether what is coming is familiar or not; after to be sure you have acquired the essence of the chapter (which you can check by looking over the discussion questions at the end of each chapter). **Boxes** are used to draw attention to particular topics, often ones that relate to more than one chapter. **Interviews** with active researchers, conducted in 1998–1999, and included in the third edition, have been updated for this edition by adding a Web site and a sample recent publication. We find these interviews valuable guides to where different fields were perceived to be moving. Comparing them with the text shows vividly how rapidly studies on evolution are progressing.

Much more information and analysis is available on all the events and concepts discussed than we could possibly have included in the book. Access to information in particular chapters is gathered together in two ways: as a list of **recommended reading** at the end of each chapter; and, at the end of the book in a **single list of literature cited** in each chapter and sources for the figures.

We have two major reasons for including references to the primary literature. One is intrinsic in the nature of the subject matter. Evolution is a science, and as such, you as the reader of this scientific textbook should not take our representations and interpretations of scientific research for granted. As you should be able to check the primary literature for yourself, we have cited enough of that primary literature to enable you to enter it with ease. Rejection or acceptance of a scientific hypothesis is based on whether data gathered to test the hypothesis refute it or not. Thus, the sequence of hominin, primate-like fossils extending from the far past to the present supports the hypothesis that humans have a primate origin (Chapter 20). Similarly, correspondence in the amino acid sequences of myoglobin and hemoglobin supports an evolutionary relationship between them (Chapter 12).

The second reason is that whether this book is used for an introductory or a more advanced class — and it is, in our view suitable for either — the primary literature cited provides an ideal basis for tutorials, discussions, essays and/or presentations.

Part I takes the publication in 1859 of *The Origin of Species by Means of Natural Selection* by Charles Darwin as the starting point. An oft-recommended version is the facsimile of the first edition published by Harvard University Press under the editorship of Ernst Mayr in 1964 (Darwin, 1964) and as an inexpensive paperback in 2005. Project Gutenberg Online Book Catalog has many of Darwin's books downloadable in reliable text form (http://www.gutenberg.org/).

An effective way to access Darwin's writings and commentaries on his work and influence, is through the *Norton Critical Edition* (Appleman, 2001), which contains an introduction by Philip Appleman, an evaluation of Darwin's life by Ernst Mayr, selections from Darwin's writing, reprints of eight essays on scientific thought before Darwin, and almost 100 commentaries on Darwin's influence on science, social thought, philosophy, ethics, religion and literature.

The following **encyclopedias, texts** and **collections of essays** are recommended, either because they cover evolution in its entirety or because they cover a major aspect of evolution.

Appleman, P, (ed.), 2001. *A Norton Critical Edition.* Darwin: Texts, Commentary, 3rd ed. W. W., New York.

Bowler, P. J., 2003. *Evolution: The History of an Idea,* 3rd ed. University of California Press, Berkeley, CA.

Browne, E. J., 1995. *Charles Darwin: Voyaging.* Alfred A. Knopf, New York.

Browne, E. J., 2002 *Charles Darwin: The Power of Place. Volume II of a Biography.* Alfred A. Knopf, New York.

Evolution, 2006. A Scientific American Reader. The University of Chicago Press, Chicago.

Hall, B. K., and W. M. Olson (eds.), 2003. *Keywords & Concepts in Evolutionary Developmental Biology.* Harvard University Press, Cambridge, MA.

Jones, S., R. D. Martin, and D. R. Pilbeam (eds.), 1996. *The Cambridge Encyclopedia of Human Evolution.* Cambridge University Press, Cambridge, England.

Keller, E. F., and E. A. Lloyd, 1992. *Keywords in Evolutionary Biology.* Harvard University Press, Cambridge, MA.

Knoll, A. H., 2003. *Life on a Young Planet: The First Three Billion Years of Evolution on Earth.* Princeton University Press, Princeton, NJ.

Niklas, K. J., 1997. *The Evolutionary Biology of Plants.* The University of Chicago Press, Chicago and London

Supplements to the Text

Jones and Bartlett offers an array of ancillaries to assist instructors and students in teaching and mastering the concepts in this text. Additional information and review copies of any of the following items are available through your Jones and Bartlett sales representative, or by going to http://www.jbpub.com/biology/.

For the Student

Developed by Dr. Bill Brindley of Utah State University exclusively for the fourth edition of *Strickberger's Evolution,* the companion Web site, http://biology.jbpub.com/evolution, offers a variety of resources to enhance understanding of evolution. The site contains a free on-line study guide with chapter outlines, quizzes and exercises to test comprehension and retention and an interactive glossary. This site also has links to other interesting and informative Web sites and seminal papers in the field of evolution.

For the Instructor

Compatible with Windows and Macintosh platforms, the Instructor's ToolKit—CD-ROM provides instructors with the following traditional ancillaries:

- The *Test Bank* of over 800 questions is available as MSWord or Rich Text Files.
- The *PowerPoint™ Image Bank* provides the illustrations, photographs and tables (to which Jones and Bartlett holds the copyright or has permission to reproduce digitally) inserted into PowerPoint slides. You can quickly and easily copy individual images or tables into your existing lecture slides.
- The *PowerPoint Lecture Outline Slides* presentation package provides lecture notes and images for each chapter of *Strickberger's Evolution*. Instructors with Microsoft PowerPoint software can customize the outlines, art and order of presentation.
- Extra *problems* and *exercises* to enhance your students' comprehension of and appreciation for the material in the text.

Acknowledgements

We are most grateful to Virginia Trimble for providing a new chapter (4) on cosmology and the origin of chemical elements and to June Hall for her contributions to Chapters 4 and 25. The finished textbook has benefited enormously from June Hall's keen editorial eye as she read through the entire manuscript at least twice. Sina Adl and Alastair Simpson provided many helpful comments on the topics of Chapters 6 to 8 and 12. Garland Allan, Gordon McOuat and Jan Sapp provided helpful comments on the comparative scientific and writing styles of Gregor Mendel and Charles Darwin. Mark Johnston provided insights into a number of aspects of fertilization in plants (Chapter 14); Marty Leonard did the same for clutch size in birds. For providing a place of solitude in which initial editing was done, BKH thanks Clive and Linda Bedford-Brown of Subiaco, Western Australia. Some of the figures were drafted by Lisa Budney and Tim Fedak; our thanks to you both. Lisa Budney also provided helpful insights into ways to present relationships, phylogenies and cladograms.

The following individuals, each a specialist in evolutionary biology, in a particular area of evolutionary biology and/or who teach evolution, took time from their academic schedules to comment on drafts of chapters or boxes (in parentheses below) for this edition. We appreciate your insights and forthright comments:

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Pat Wise, University of Calgary (18)
Nate Young, Stanford University (20)

The index is a vital part of any book and especially of a textbook. A colleague who prepared the index for a book that he had just finished writing was surprised to see a theme emerge in a set of entries, a theme he was not conscious of having developed in the book. We had the index "test-driven" by a number of colleagues in different areas of evolution. We asked them to check that the index provided the entries they would expect to find and in the places they would expect to find them. This valuable exercise resulted in additional entries and cross-references, both of which enhance the utility of the index. We thank Chris Corkett, Mark Johnston, Alan Pinder, Wendy Olson and Liz Welsh for their dry runs on the index.

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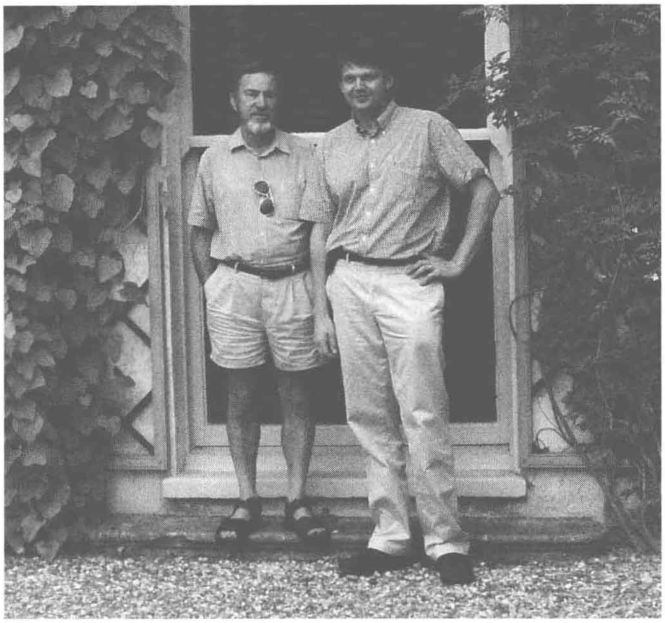
October 2007

About the Authors



Brian Hall (left) and Benedikt Hallgrímsson (right) photographed outside Charles Darwin's home, Down House, in July 2006 after having participated in the symposium on *Tinkering: The Microevolution of Development,* held at the Novartis Foundation in London.

Brian Hall, born, raised and educated in Australia, has been associated with Dalhousie University in Halifax, Nova Scotia since 1968, most recently as a University Research Professor and George S. Campbell Professor of Biology, and since July 2007 as University Research Professor Emeritus. He was Killam Research Professor at Dalhousie University (1990–1995), Faculty of Science Killam Professor (1996–2001) and Canada Council for the Arts Killam Research Fellow (2003–2005).

Trained as an experimental embryologist, for the past 40 years he has undertaken research into vertebrate skeletal development and evolution and played a major role in integrating evolutionary and developmental biology into the discipline now known as *Evolutionary Developmental Biology (evo-devo);* he wrote the first evo-devo text book, published in 1990 and in a second edition in 1999 (Hall 1999a).

A fellow of the Royal Society of Canada and Foreign Honorary Member of the American Academy of Arts and Sciences, Dr. Hall has earned numerous awards for his research, teaching and writing, including the 2005 Killam Prize in Natural Sciences, one of the top scientific awards in Canada.

Benedikt Hallgrímsson was born in Reykjavík, Iceland, and completed his studies at the University of Alberta and the University of Chicago. A biological anthropologist and evolutionary biologist, he combines developmental genetics and bioinformatics with morphometrics to address the developmental basis and evolutionary significance of phenotypic variation and variability. His work has focused on humans and other primates as well as mouse models and has employed both experimental and comparative approaches to study the evolutionary developmental biology of variation. He is the editor-in-chief of *Evolutionary Biology,* a journal dedicated to the synthesis of ideas in evolutionary biology and related disciplines.

Based at the University of Calgary, Dr. Hallgrímsson teaches organismal biology and anatomy. There he has received several Gold Star Teaching Awards, a Letter of Excellence Lecturer Award and the McLeod Distinguished Achievement Award. He is featured on the University of Calgary "Great Teachers" website. From the American Association of Anatomists, he received the Basmajian/Williams and Wilkins Award for educational contributions in 2001.

Drs. Hall and Hallgrímsson have worked together over many years. Their latest completed collaboration before this text is the edited volume *Variation: A Central Concept in Biology* (2005), which addresses a concept of fundamental importance in evolutionary biology. The late Ernst Mayr concluded his foreword to the book with "In short, variation is an endless source of challenging questions."

Answering Life's Timeless Questions

Where do we come from? What are we? Where are we going?

—Translation of the title *D'où venons nous? Que sommes nous? Où allons nous?* one of Paul Gaugin's most famous works, perhaps his ultimate masterpiece, in which he depicts his vision of life's great questions.

There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed laws of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being evolved.

—The last sentence of *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, by Charles, Darwin, 1859.

Darwin's alienation of the inside from the outside was an absolutely essential step in the development of modern biology.... The time has come when further progress in our understanding of nature requires that we reconsider the relationship between the outside and the inside, between organism and environment.

—From *The Triple Helix: Gene, Organism, and Environment* by Richard Lewontin, 2000.

PART 1

The Historical Framework

Evolution as Science

It has become common to acknowledge that our views of the world are strongly influenced by the culture in which we grow up. That is, different cultures place different emphases on how people perceive various events and relationships and on how they explain these perceptions. Thus, in one culture death is a recycling of a person's spirit into another organismic form; another culture believes death is a state of reward and punishment for an individual's behavior, while still another culture regards death as the end of a person's existence.

What we consider science is also culturally dependent in the sense that large differences can exist between cultures as to whether or how scientific concepts are applied to natural events. Explanations that many of us accept as scientific — analyses based on rational, understandable principles and laws — others do not necessarily accept, or accept to varying degrees. Thus, some people consider that human behavior and interactions can be explained by natural processes; others believe these are predestined actions produced by one or more godlike creators; and still others propose that events are determined by constellations of planets, stars and phases of the moon that have mysterious powers and properties.

In general, nonliving phenomena have been considered more acceptable to scientific analyses in Western European culture than matters that touch on life itself, and on human life in particular. For example, physics and chemistry were well established as sciences by the nineteenth century, whereas biology, especially evolutionary approaches, was the subject of vitalistic interpretations by biologists in the past and by various religious groups even to this day.

A philosophical criticism sometimes raised against evolution as a science is that evolutionary explanations (hypotheses) cannot be tested and supported in the same fashion as hypotheses in physics and chemistry. The claim is made that because evolutionary studies deal with *events that occurred in the past* — events that are generally impossible to repeat in a laboratory — evolutionary biology can never reach the status of such sciences as physics and chemistry. Some critics extend these arguments to paleontology, geology and astronomy, three fields of study also dealing with the past and with matters on such a large scale that they cannot be repeated experimentally in the laboratory. Another criticism mounted against evolution claims that many studies designed to demonstrate evolution cannot be properly evaluated by the scientific method.[1]

Rejection or acceptance of a scientific hypothesis is based on whether data gathered to test the hypothesis refute it or not. Hypotheses constructed so they can never be refuted ("falsified," according to the philosopher Karl Popper) are not considered scientific.[2] Thus, concepts that invisible angels are responsible for the birth or death of an organism, or that God created the universe, are not scientific. Any events that seem to conflict with such a concept can always be reinterpreted to support it. Some claim that because evolutionary concepts are historical, they appear

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[1] *Ways of Knowing* by Pickstone (2001) contains a unified argument against such criticisms in an analysis of the development of the scientific method in science, technology and medicine, an analysis described by the late Roy Porter as, "the most exciting synthesis we now possess."

[2] A number of philosophers of science have noted that naïve falsification is not always sufficient to distinguish scientific from nonscientific theories. As their example: if we took Popper's definition seriously, then Newton's inverse square law would be utterly unscientific because it cannot be refuted.

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