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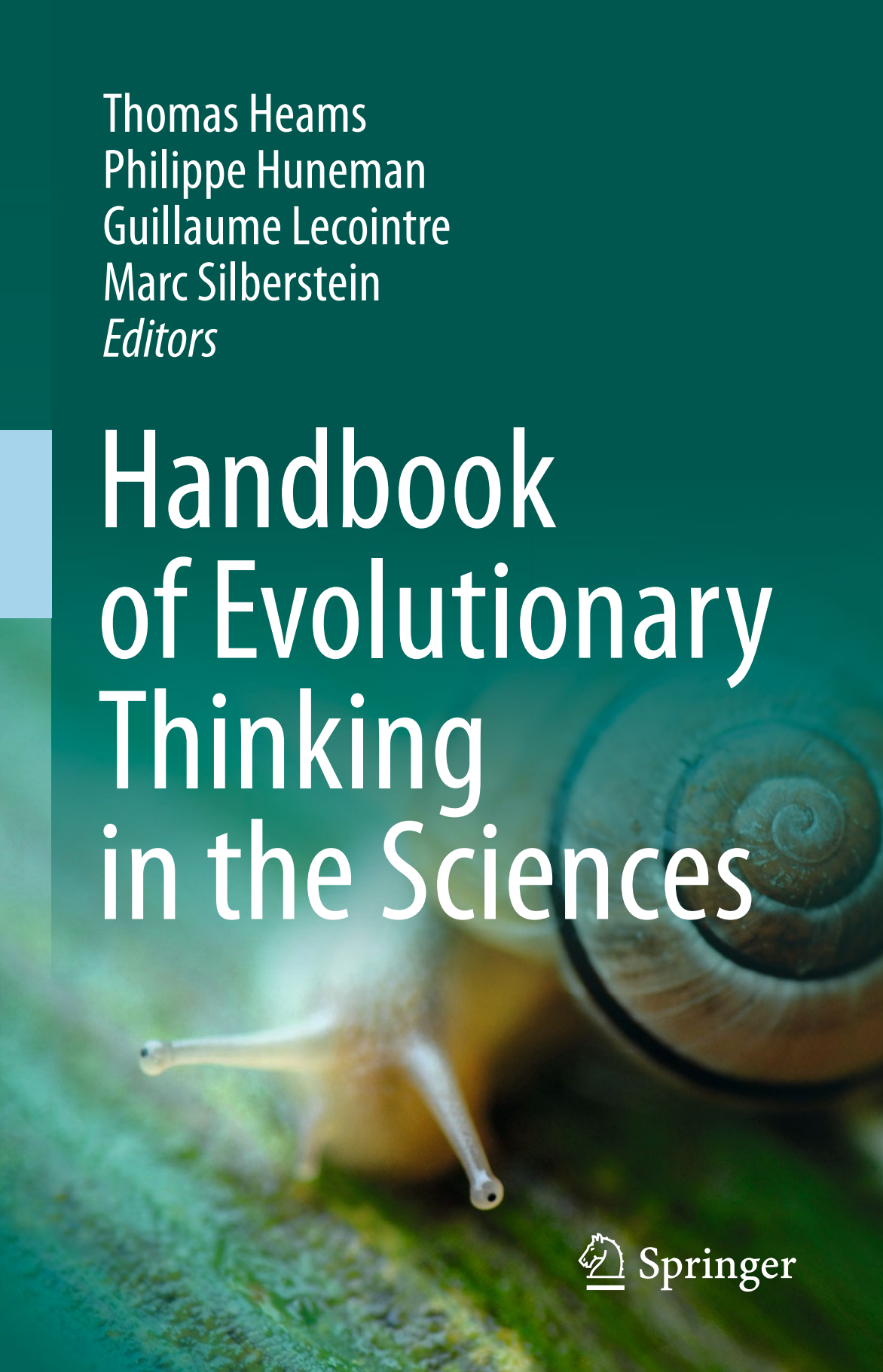
Editors

Handbook of Evolutionary Thinking in the Sciences



Springer

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Editors
Thomas Heams
INRA, UMR 1313, Génétique Animale
et Biologie Intégrative
Jouy-en-Josas cedex, France

Département Sciences de la Vie et Santé
AgroParisTech
Paris cedex 05, France

Guillaume Lecointre
Museum National d'Histoire
Naturelle (MNHN)
Paris, France

Philippe Huneman
Institut d'Histoire et de Philosophie des
Sciences et des Techniques
CNRS/Université Paris I Sorbonne/ENS
Paris, France

Marc Silberstein
Editions Matériologiques
Paris, France

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Foreword

Whatever its importance, the book Darwin published under the title *On the Origin of Species* probably did not enjoy such astounding success as one often reads in the innumerable books and articles about him. The legend has it that the first edition sold out on the day of publication, November 24, 1859, as Darwin hinted in his diary: "The 1st. Edit was published on Nov^{r}. 24th & all copies ie 1,250 sold first day." (*Darwin's Journal [1809–1881]*, CUL-DAR158.37 verso, quoted in *Darwin Online*, http://darwin-online.org.uk/). In fact, the publisher, John Murray, had shipped copies to booksellers throughout the country on November 22, but nothing is known about when they were actually bought in the shops.[1]

Whatever the case, the present work, for which I have the pleasure of writing the preface, appeared in French around the 150th anniversary of the *Origin*. Its editors so intended it, to celebrate the anniversary of this work, which has been as much or more celebrated than the 200th anniversary of Darwin's birth (February 12, 1809), which was itself abundantly celebrated throughout the world in 2009. They are right: it is less the man himself than his immensely fruitful theoretical contribution that merits celebration, and, even more, reflection, from the standpoint of today's questions and knowledge. As Pascal Tassy writes in this volume, "The Darwinian heritage is a formidable edifice of unextinguished controversies, continually coming back to life, being augmented, made more complex."

There is no better way of introducing this lively, argumentative book than to explain a few words about its inception. Only afterward will I discuss its intellectual objectives. In fact, however, it is only in the last part of the work that the context that motivated it is revealed, after a 1,000 pages of theoretical debates. This context has three components. First, the work results from the spectacular resurgence of tensions between evolutionary science and religion. Although the chapter by d'Olivier Brosseau and Marc Silberstein on the various cloaked forms of creationism today is the only one on this subject in the book, it nevertheless expresses, beyond a doubt, an intellectual and political disquiet widely shared among the authors. The second

[1] See R.B. Freeman's introduction to the 1859 edition of *On the Origin of Species* http://darwin-online.org.uk/EditorialIntroductions/Freeman_OntheOriginofSpecies.html.

element, also very concrete, is teaching. While evolutionary sciences are solidly supported in school curricula, teachers, as Corinne Fortin explains, are particularly ill at ease. Indeed, aside from a feeling that they themselves have not fully mastered the necessary content, they are reluctant to engage with the questions of pupils on a subject that is not always socially neutral. The final element of the book is immediately specified in the introduction: it concerns the controversial relations existing today between the natural, and particularly the biological, sciences and the human sciences.

These three fields of play provide more the scenery than the subject of the book. Aside from the two final chapters that I have just mentioned, the book is not an inquiry into the relationship between evolution and science nor into the teaching of evolution nor even into the status of the human sciences, although this last theme is present as a sort of filigree throughout a significant part of the work. Rather than placing these questions of culture, politics, and ideology front and center, the editors have preferred to show evolutionary science as it is today, with its immense fecundity, but also with the questions and the internal debates running through it. With regard to the contexts we have just been discussing, the book leaves something of an aerial impression. To those who want in the name of religion to rip open politics or war in the human sciences, it responds with a 1,000 pages of dense studies, where the reader is invited to discover reason at work. The book is difficult, since it launches without concession into difficult theoretical problems, where often no consensus exists. But it is just this that makes it light and plants it in the antipodes to what Gaston Bachelard called "heavy thinking" (*les pensées lourdes*) – thought which isn't really thinking, but opinions founded on hearsay and prejudice.

You understand, then: religion, teaching, and the human sciences provide the scenery of the work, in the theatrical sense. The scenery could have been different; the texts would have been the same. This is the great quality of this book: far from Darwinian hagiography and self-justifying commemoration, it invites the reader to enter the contemporary forest of the theory of evolution, of its underpinnings, and of its effects on contemporary knowledge of evolution, *its* underpinnings, and its effects on knowledge in general.

I will here add some words on the place and on the persons, before coming to the subject of the piece. This book was originally published in French, and by authors who were mostly Francophones. This is also exhilarating. Darwinian thinking is in France no longer so incongruous that it is necessary either to convene French researchers to question it or to resort to foreign authors to discuss it. This is undoubtedly the result of an evolution whose beginnings lie in the postwar period. Indeed, it was at that time that powerful scientific traditions began to develop in our country, first in population biology, then in theoretical paleontology, and today represented by an impressive cohort of young researchers. I must observe here that three fifths at least of the authors who have participated in this volume fall into the category of "junior researchers," and in fact often are very young scholars.

Now I come to the substance of the book. Its objective is, as the expression in the introduction has it, to "cover Darwinism in all its forms." It is nevertheless worth specifying that its objective is not historical: it is modern Darwinism as it inspires

present-day scientific research that it treats, not Darwinism in its historical scientific or cultural guises. I would like to mention the French original title of the book, *Les Mondes darwiniens* ("Darwinian worlds"). I agree that this title could hardly be kept for the English translation; *Handbook of Evolutionary Theory in the Sciences* is perfectly appropriate. However, the idea of a number of "Darwinian worlds" had something appealing. The Darwinian worlds alluded to by the editors are the realms of current research: they referred to a number of fundamental concepts, research programs, controversies, unresolved questions, and even possible future paths of investigation. Although the authors have taken care to specify the sense in which they are referring to Darwin in the subjects they are examining, it is clear that it is the present and the future of the researches collectively called "Darwinian" that matter to each of them.

I will here sketch out a taxonomy of the types of theoretical Darwinism deployed in this *Handbook of Evolutionary Theory in the Sciences*. Two distinctions will be enough. The first draws on the two components of the theory Darwin proposed in the *Origin*: "descent with modification" and "natural selection." The second concerns the uses of them made by those who, after Darwin, claimed to represent him as evolutionists. I propose distinguishing two lines of development of the fundamental Darwinian principles: the first consists of revising or refounding those principles, the other of deploying them in practice. I will call these two lines "expansion" and "extension," respectively.[2] They are by no means mutually exclusive, on the contrary.

In the light of this distinction, the theoretical intentions of this volume appear clearly. In the first place, I observe that the work has taken care to accord equal importance to the two components of Darwin's original theory, namely, the hypothesis of "descent with modification" (the idea of a genealogical nexus of all living beings, in all the immensity of time and space in which they are transformed) and the hypotheses of variation and natural selection (the processes that ultimately explain and largely control evolutionary change for Darwin). This equal attention to the two principles is unusual: too often, in Darwinian celebrations, we see a tendency to neglect the formidable theoretical difficulties raised by phylogenetic reconstructions and to take more interest in selection. Certainly, the difficulties

[2] I here make use of the terms of the late S.J. Gould, although for a different purpose. In his scientific testament (*The Structure of Evolutionary Theory*, Cambridge: Harvard UP, 2002), he maintained that the contemporary theory of evolution could not be interpreted as either an "extension" of the Darwinian framework (Darwinian principles applied to a wider spectrum of phenomena) or as a new theoretical framework that would "replace" the earlier one, by virtue of a drastic paradigm shift (which would imply that the principles would be radically different). Gould preferred to speak of "expansion" of the theoretical Darwinian framework, in the sense that the same principles remained central, but had been "reformulated" in such a way as to give the entire edifice an entirely different appearance. (For more details on this unusual distinction between "extension" and "expansion," see J. Gayon, "Mort ou persistance du darwinisme? Regard d'un épistémologue," in *C.R. Palevol.*, 8 (2009): 321–340). I am here picking up the distinction "extension/expansion" while emancipating it from Gould's particular usage, and I contend that the two fundamental principles of Darwinism (descent with modification and selection) have been simultaneously extended in their usage and revised in their fundamentals.

raised by phylogenetic inference were fully understood only in the second half of the twentieth century. But this is an essential dimension of contemporary Darwinism that well reflects the now-commonplace distinction between *patterns* (the fundamentals of phylogenetic reconstructions) and *processes* in evolution (for example, variation and selection). This distinction between patterns and processes permeates the entire volume. It is explicit in the first part, which analyzes fundamental concepts, but it is also to be found in the two succeeding parts, where the engagement with Darwinism does not mean only, nor exclusively, the explanation of evolution by means of natural selection.

In the second place, the volume examines, exceptionally systematically, the various modes of expansion and extension of the two Darwinian principles. As I observed above, I understand by "expansion" a deepening of the foundations, which may require important revisions. This is a characteristic of great scientific theories that is too seldom underlined: they do not last forever because they are periodically refounded. By "extension," I mean the growth of the domain of phenomena to which Darwinian principles have been applied. Discussion in detail of these two lively regimes in contemporary evolution would be inappropriate here; I ask the reader to pardon me for leaving the schema as a suggestion. The expansion (or revision) of the Darwinian framework has been particularly spectacular in the following cases:

1. Numerous authors ask whether reproduction and heredity are essential ingredients for the concept of natural selection. The breadth of disagreement on this point is impressive. Whereas some researchers argued for an enlargement of the concept, which would make differential reproductive success a merely facultative form of differences in fitness, and thus of the process of natural selection, the majority of authors of this book argue for the orthodox classical version and distrust the loss of operationality represented by the elision of any reference to reproduction and heredity in the principle of natural selection. This question is closely linked to that of units and levels of selection, which has preoccupied evolutionists for the last three or four decades. It is clear that if the postulate of heritability of fitness is weakened (and thus the necessary conclusion that the principle of natural selection can only be applied to entities capable of reproduction), the spectrum of entities (natural, cultural, or artificial) to which natural selection can be applied is greatly enlarged. We may recall here that this debate has in fact existed since the very beginnings of Darwinism. It was one of the issues in play in the debate between Darwin and Spencer about whether the principle of natural selection was *a priori* or not.
2. Since the 1970s, the debate about the units of selection has laid great importance on the notion of "replication." A replicator is an entity whose structure can be copied into another entity. The gene is the paradigmatic example of a replicator. An organism, in contrast, is not a replicator: it reproduces itself (that is, it can beget a being of the same sort as itself), but the being thus begotten is not a "copy." This notion of replication has gotten the better of that of reproduction for numerous authors, biologists, and philosophers. Yet, extensions of Darwinism beyond the biological domain, where using the concept of replication ceases to

be self-evident, clearly challenge classical views of replicator and selection, since they often can't make room for discrete replicators.

3. Finally, I would like to underline the importance that numerous authors (notably Christophe Malaterre and Francesca Merlin) confer to stochastic factors and more generally to the workings of chance. This theme is of course not new. Since the end of the nineteenth century, sampling effects and chance have been a theme of recurrent interest as a possible important factor in evolution. What is new is the contemporary debate over dawning awareness of the enormous difficulty, even the theoretical impossibility, of differentiating in practice between stochastic and selective effects. Numerous authors (notably Julien Delord and Arnaud Pocheville) question the growth in influence of stochastic models in evolutionary ecology.
4. It is nevertheless in the modern treatment of phylogenetic inference (returning to "descent with modification" in the Darwinian theory) that the most impressive revisions have been produced over the course of the last half century. As the contributions of Guillaume Lecointre and Pascal Tassy convincingly show, phylogenetic inference is no longer today an "art" founded solely on individual expertise; it is rather a science furnished with reproducible operational principles. In this case, it is certainly not proper to speak of a "revision" of the Darwinian principle of "descent with modification"; the subject instead represents an entire branch of science that has developed methods of which Darwin and his successors had no inkling. The chapters devoted to this subject are particularly impressive (Véronique Barriel, Guillaume Lecointre, Pascal Tassy).

The volume examines other paths of revision of the fundamental principles of Darwin that I cannot discuss here. It is clear that current experimental biology, notably molecular biology, genomics, and developmental biology, is opening important perspectives on the question of constraints on the sources of variation and, thus, of the very power of natural selection.

As for extensions of the Darwinian theoretical framework to new objects, this *Handbook of Evolutionary Theory in the Sciences* provides an impressive harvest. I would like here to distinguish two of them. One consists in mutually applying Darwinian principles to novel biological objects; the other consists in transposing them to fields of phenomena not specifically biological, or at least not obviously biological.

In the first category, I may mention the application of the principle of descent to the paths of biochemical synthesis or degradation, which is referred to in Lecointre's chapter on descent. The volume elsewhere examines numerous examples of the extension of the principle of natural selection to levels of organization or to biological phenomena other than those considered by Darwin or the modern synthesis: behavior (Henri Cap), embryology and developmental systems (Alan Love, Antonine Nicoglou), the origin and maintenance of sex (Pierre-Henri Gouyon, Tatiana Giraud, Damien de Vienne), medicine (Pierre-Olivier Méthot), and ecology (Julien Delord, Arnaud Pocheville). The portions of the volume dealing with evolutionary psychology (Stephen M. Downes, Pierre Poirier and Luc Faucher, Pierrick Bourrat), evolutionary ethics (Christine Clavien, Jérôme Ravat), the origin of language (Jean-Louis Dessalles), and teleosemantics (Françoise Longy) move also in this direction.

The second form of extension consists in a transposition of Darwinian principles into domains that are claimed to be analogous. Three spectacular examples are examined. The first is that of historical linguistics, where the quantitative methods of phylogenetic inference have recently been transposed and applied to the question of phylogeny of languages (Mahé Ben Hamed). The second example is that of evolutionary economics, which uses a principle of "economic natural selection" (Eva Debray). The last example of transposition is that of robotics, which has found in "evolutionary algorithms" a remarkably efficient conceptual tool, in favor of more and more powerful means of calculation (Marc Schoenauer, Nicolas Bredeche).

Of course, these two forms of extending Darwinism, literal and analogical, are not watertight. Evolutionary ethics, for example, oscillates between one and the other, and the same is true of evolutionary teleosemantics. In the case of cultural evolution (Christophe Heintz and Nicolas Claidière), the two approaches are inextricably intertwined.

This taxonomy of modes of expansion (theoretical) and of extension (phenomenal) of Darwinism does not exhaust the material of this book, which questions also the often-difficult relations between evolutionary and functional biology. Even if the majority of biologists are in agreement with Dobzhansky's formulation, according to which "Nothing in biology makes sense except in the light of evolution," vast expanses (in fact, the majority) of biological research remain that follow their course without strong relations with evolutionary theory. I am struck by the skeptical reflection of authors who, in this volume, have reflected on the relationships between molecular biology and evolution (Michel Morange), between developmental biology and evolution (Guillaume Balavoine), between systems biology and evolution (Pierre-Alain Braillard), and between synthetic biology and evolution (Thomas Heams). As far as biomedical research is concerned, it is clear that in spite of the interest raised by "evolutionary medicine," biomedicine remains to a great degree outside of the field of evolution.

This wonderful book, unique in the literature, is therefore distinguished by its combination of systematizing and openness. On finishing it, one is convinced by the inanity of the question of whether one should be a Darwinian or not. Darwinian principles have been, and in fact are now, exceptionally fertile in numerous fields of biology, anthropology, and technology. But it is also clear that Darwinism cannot explain everything. It exhausts neither biology nor the human or social sciences nor, obviously, technology. Nevertheless, it would be venturesome, and without a doubt irresponsible from a cognitive point of view, to want to pass it up.

This leads me back to the contextual elements I mentioned at the beginning of this foreword. Among these, I mentioned teaching. This volume does not lack for ambition in this regard. I have not tried to analyze here the nine chapters on "concepts" that open the work. They offer methodological and philosophical reflections on concepts such as variation, heredity, natural selection, function, and descent. But I must underline the demanding level at which they are written. The reader must not be surprised: these liminal chapters are probably the hardest, since they attempt to define the sense and the limits of these fundamental terms, without which the theory of evolution is not possible. It is not one of the weak points of this book that it puts

these difficult chapters dealing with the terminological and conceptual apparatus of evolution up front. Anyone who thinks that the Darwinian approach to evolution is trivial will there be convinced of the effort of thought that it demands to implement it.

IHPST/Université Paris 1 Sorbonne, Jean Gayon
13 rue du Four, 75006 Paris, France

Contents

Contributors

Guillaume Balavoine Institut Jacques Monod, CNRS/Paris Diderot University, Paris, France

Anouk Barberousse History and Philosophy of Science, Lille University, Lille, France

Véronique Barriel Départment Histoire de la Terre, UMR 7207, MNHN/UPMC/CNRS, Centre de recherche sur la paléobiodiversité et les paléoenvironnements, Muséum national d'histoire naturelle, Paris, France

Mahé Ben Hamed Databases, Corpora & Language Lab (Bases, Corpus, Langage-UMR 7320), CNRS, Nice, France

Pierrick Bourrat Department of Philosophy, University of Sydney, Sydney, Australia

Pierre-Alain Braillard Independent Scholar, Peyregrand, Drulhe, France

Nicolas Bredeche ISIR Université Pierre et Marie Curie, Paris, France

Olivier Brosseau Editions Matériologiques, Paris, France

Henri Cap Department of Zoology, Natural History Museum of Toulouse, Toulouse, France

Pascal Charbonnat Université Paris Ouest Nanterre La Défense, IREPH, Nanterre, France

Nicolas Claidière Laboratoire de psychologie cognitive, Université d'Aix – Marseille, CNRS, Fédération de recherche 3C, Marseille cedex, France

Christine Clavien Department of Ecology and Evolution, University of Lausanne UNIL-Sorge, Bâtiment Biophore, Lausanne, Switzerland

Armand de Ricqlès Historical Biology and Evolutionnism, Collège de France, Université Paris VI, UMR 7179, Paris cedex 05, France

Damien de Vienne Laboratoire de Biométrie et Biologie Evolutive, CNRS UMR 5558, Paris, France

Eva Debray Laboratoire SOPHIAPOL (EA 3932), Université Paris Ouest, Nanterre, France

Julien Delord Pres Hesam, Institut d'Histoire et de Philosophie des Sciences et des Techniques, (CNRS UMR8590), Université de Paris, Paris, France

Jean-Louis Dessalles Artificial Intelligence and Cognitive Modelling, Telecom ParisTech, Paris, France

Stephen M. Downes Professor and Chairman, Department of Philosophy, University of Utah, Salt Lake City, UT, USA

Luc Faucher Département de philosophie, Institut des Sciences Cognitives, Centre Interinstitutionnel de Recherche en Sciences et Technologies, Université du Québec à Montreal (UQAM), Montréal, Canada

Université du Québec à Montreal (UQAM), Montréal, Canada

Corinne Fortin STEF ENS Cachan/Institut français d'éducation (IFE) ENS Lyon, Lyon, France

Jean Gayon Institut D'histoire Et De Philosophie Des Sciences Et Des Tecniques (Cnrs Umr8590), Université Paris I Panthéon Sorbonne, Paris, France

Tatiana Giraud Laboratoire Ecologie, Systématique et Evolution, UMR 8079 CNRS-UPS-AgroParisTech, Paris, France

Université de Paris-Sud, Orsay cedex, France

Pierre-Henri Gouyon Département Systématique et Evolution, Muséum national d'Histoire naturelle, CP39, UMR 7205 CNRS "Institut de Systématique, Evolution et Biodiversité", Paris Cedex 05, France

Philippe Grandcolas UMR 7205 CNRS, Institut de Systématique, Evolution et Biodiversité, Muséum National d'Histoire Naturelle, Paris, France

Thomas Heams INRA, UMR 1313, Génétique Animale et Biologie Intégrative, Jouy-en-Josas cedex, France

Département Sciences de la Vie et Santé, AgroParisTech, Paris cedex 05, France

Christophe Heintz Department of Cognitive Science, Central European University, Budapest, Hungary

Philippe Huneman Institut d'Histoire et de Philosophie des Sciences et des Techniques, CNRS/Université Paris I Sorbonne/ENS, Paris, France

Guillaume Lecointre Département Systématique et Evolution, Muséum national d'Histoire naturelle, CP39, UMR 7205 CNRS "Institut de Systématique, Evolution et Biodiversité", Paris Cedex 05, France

Françoise Longy Institut d'Histoire et de Philosophie des Sciences et des Techniques (IHPST), Université de Strasbourg, Paris, France

Alan C. Love Associate Professor of Philosophy, Director, Minnesota Center for Philosophy of Science, University of Minnesota – Twin Cities, Minnapolis, MN, USA

Edouard Machery Department of History and Philosophy of Science, The University of Pittsburgh, Pittsburgh, PA, USA

Christophe Malaterre Département de philosophie, UQÀM, Montréal, QC, Canada

Francesca Merlin Institut d'Histoire et de Philosophie des Sciences et des Techniques (IHPST), CNRS/Université Paris I Sorbonne, Paris, France

Pierre-Olivier Méthot Faculté de Philosophie, Université Laval (Québec), Québec, Canada

Centre interuniversitaire de recherche sur la science et la technologie (CIRST), Université du Québec à Montréal, Montréal, Canada

Michel Morange Centre Cavaillès, République des savoirs: lettres, sciences, philosophie, USR 3608, Paris Cedex 05, France

Antonine Nicoglou Institut d'Histoire et de Philosophie des Sciences et des Techniques, Labex "Who Am I?" Université Paris 7, Paris, France

Arnaud Pocheville Department of Philosophy, University of Sydney, Sydney, Australia

Pierre Poirier Département de philosophie, Institut des Sciences Cognitives, Université du Québec à Montreal (UQAM), Montréal, Canada

Laboratoire d'analyse cognitive de l'information, Université du Québec à Montreal (UQAM), Montréal, Canada

Jérôme Ravat UFR de philosophie, Université Paris-Sorbonne (Paris IV), Paris, France

Sarah Samadi Muséum National d'Histoire Naturelle, Paris, France

Marc Schoenauer INRIA, CNRS, Paris, France

Marc Silberstein Independent Scholar, Editions Matériologiques, Paris, France

Pascal Tassy CR2P CNRS-MNHN-UPMC, Département Histoire de la Terre, Muséum national d'Histoire naturelle, Paris Cedex 05, France

Stéphane Tirard Professor in History of Sciences, François Viète Center in Epistemology and History of Sciences and Technology, University of Nantes, Nantes, France

Priscille Touraille Laboratoire d'Eco-Anthropologie, Muséum national d'Histoire naturelle, Paris, France

Chapter 1
Introduction

Thomas Heams, Philippe Huneman, Guillaume Lecointre, and Marc Silberstein

1859. The appearance of a *magnum opus* which revolutionizes the thought of its century, of the following, and of our own. It is a book by Charles Robert Darwin, *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. Despite its commemorative aspect[1] – the one hundred and fiftieth anniversary of the appearance of this work, the bicentenary of the birth of Darwin – it appeared important to us to give an account of the state of research that has been done in the vast domain of the "Darwinian Worlds." In effect, the Darwinian theory of evolution is evolving ceaselessly and as the work of scientists and of philosophers of science is so plethoric, so diverse, so technical, it was becoming necessary that an account of it should exist in French. Ambitious editorial initiatives aiming to cover Darwinism in all of its forms for a francophone readership

[1] The french version of this book was published in 2009.

T. Heams (✉)
INRA, UMR 1313, Génétique Animale et Biologie Intégrative, Domaine de Vilvert, 78352 Jouy-en-Josas cedex, France

Département Sciences de la Vie et Santé, AgroParisTech, 16 rue Claude Bernard, 75231 Paris cedex 05, France
e-mail: thomas.heams@agroparistech.fr

P. Huneman
Institut d'Histoire et de Philosophie des Sciences et des Techniques, CNRS/Université Paris I Sorbonne/ENS, 13 rue du Four, 75006 Paris, France
e-mail: Philippe.huneman@gmail.com

G. Lecointre
Département Systématique et Evolution, Muséum national d'Histoire naturelle, CP39, UMR 7205 CNRS "Institut de Systématique, Evolution et Biodiversité", 57 rue Cuvier 75231, Paris Cedex 05, France
e-mail: lecointr@mnhn.fr

M. Silberstein
Independent Scholar, Editions Matériologiques, Paris, France
e-mail: silbersteinm@gmail.com

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were rare indeed.[2] This is the origin of the original version of this book (entitled *Les Mondes darwiniens*, "The Darwinian worlds"), but in the end it appeared that the range of the volume, the amount of fields covered as well as the effort in presenting in details the core of the Darwinian evolutionary theory joined with the attempt to engage many hot topics often left aside from classical handbooks of evolutionary biology (e.g. synthetic biology, robotics, linguistics…) was worth publishing an english version for a wider audience.[3]

There seemed to us to be many reasons to make our enterprise of summarizing Darwinian knowledge legitimate and urgent. On the one hand, as Jacques Monod said 30 years ago, Darwinism is the canvas for all of the biological sciences. Nevertheless, even if we can intuitively agree on the unifying status of Darwinism, it is important to explain, to show, with a detailed argument, how the Darwinian design supports a fundamental unity in biology within all of its levels of integration – in other words, from macromolecules to the ecosystem. On the other hand, for many reasons, Darwinism in France introduced itself less early and less significantly than in the other European countries, both in the academic world and in general culture. Considering that many people have been working to gain on this "delay" for 20 years, it was good for a sizable publication to come and take account of it.

In the end, beyond the unity of biology, one of our preoccupations was the unity of scientific knowledge itself. Suspicion regarding Darwinism is still frequent in the milieu of the social and human sciences. If we wanted to devote many pages to Darwinian thought in these sciences (in a word, the humanities), it is because, for many anthropologists and psychologists, evolution remains something that only concerns the plants and the animals and has nothing to do with our manner of living, of feeling and thinking, with human beings themselves. The status of human beings as being exceptional accompanies this indifference to Darwinism in the humanities. By underlining the explicative power of Darwinism in regard to phenomena, behaviors, or specific types of human character (without of course wanting to say that humans can be entirely understood by these things), we wish to show that reality is not crossed by a fissure that puts humans into a vaulted position; that is to say that science is one, and that there are within it numerous regions which are governed by diverse explanatory modes and epistemological ideas, and thus we intend to move from an absolutely dualist vision of the sciences to a conception of them that is at the same time monist (without an ontological exception for humans) and pluralist (the schools of science largely exceed the dyad of "Natural Sciences/Human Sciences").

[2] Notably, P. Tort (eds.), *Dictionnaire du darwinisme et de l'évolution*, Paris, PUF, 3 vol, 1996. P. Tort (dir.), Pour Darwin, Paris, PUF, 1997. *Biologie évolutive*, Frédéric Thomas, Thierry Lefevre, Michel Raymond (eds.), Bruxelles, De Boeck, 2010.

[3] Of course, we do not pretend to exhaustivity. A no less voluminous second volume would have been necessary to fill the gaps which are inevitably here. The present book however includes original chapters, that were not in the french version.

Returning to biology. To believe certain researchers in the evolutionary sciences still some years ago, all had been said on the matter. Genetics and molecular biology gave the last word on history, Darwinism had found its experimental acme in these sciences, and the evolutionary Modern Synthesis – born in the 1930s – was on the point of being complete. But the growing importance of the epigenetic dimension in development, stochastic gene expression, phenotypic plasticity, evo-devo (a developmental theory that works in conjunction with evolution), phylogenetics and its ample reconstructions of the structure of the tree of life, scientific ecology and its efforts to integrate with evolution, the sound critiques of both naive adaptationism and an idealist vision of genes and of the "genetic program," synthetic biology and systems biology, etc., came to trouble the picture, which ultimately turned out to be incomplete.

One of the objectives of this book is to trace the contours of these paths of research in their full richness by visiting the grand axes and themes within the field of evolutionary biology since its blossoming in the 20th century. In this frame, we fully claim the usage of the word "Darwinism," as we also do within our discussions of the actual state of the theory, with its multiple extensions and prolongations, its reticulated aspect.[4] Far from pejorative meanings and ideological suspicions, "Darwinism" must be understood here as a scientific approach towards both dynamics and the history of the real world that was founded more or less directly on the links between variation, heredity, and natural selection – in which chance plays a central role (i.e. in the modern sense even including neutralism and non selective effects of genetic drift). Thus, the "ism" is justified by the fecundity of the approach and the importance of exploring its limits. Metaphorically, the evolution of (the theory of) evolution is tangled; in regards to both the diversity and the density of its internal extensions as in its developments outside of the initial field. This term "Darwinism" is moreover often the one that is used by its followers, and is therefore *de facto* a *semantic crossroads* which justifies in part the enterprise of this book. In the end, this word is so frequently corrupted, at the risk of discrediting the central work itself – notably when it is fallaciously assimilated by the caricatures which surround it, like "Social Darwinism," or even racism – that it seemed necessary to us to not leave it in the hands of doubters who are unconcerned with accuracy.

Before showing the recent developments in the expanding world of Darwinism, we have devoted a part (Parts 1 and 2, "**Concepts**") of the book to the principal ideas which run through the field of evolutionary biology: variation, heredity, selection, adaptation, function, character, species, descent (filiation), life. All of these notions are in effect constantly at play within the ensemble of the book; and to have an understanding of them is necessary in order to appreciate the details of the more specialized chapters. This is to say that although some other ideas could have had a chapter dedicated to each of them, they are instead approached, brought up or treated – according to the case – in the notional chapters of this first part, or sometimes in the chapters of parts 3 to 5. Thus, for example, homology (and its counterpart,

[4] The linear structure of a book does not permit us to adequately take account of this. However, we have inserted numerous cross-references in the chapters which will permit the reader to "navigate" a vast resource of interconnected ideas that are spread throughout the book.

homoplasy), a crucial idea in the evolutionary sciences – since they are comparative sciences – is for the most part examined in the notional chapters "Descent (Filiation)" and "Character." It is the same with, among others, the ideas of resemblance or of global similitude, of optimality, of ontogeny, of chance, etc., as they are approached or explained in numerous other chapters.

We have next grouped together the chapters concerning the actual and progressional state of the theory of evolution in Parts 3 and 4: "Darwinism in Progress." Part 3 ("Philosophy of Science") brings up the epistemological qualities of the new research, while showing the acuity of the questioning of the modes of reasoning proper to the domain of evolutionary biology, as well as the interactions between scientific disciplines and between those of the philosophy of biology (of course, these epistemological questions are constantly present in the notional chapters of Part 1). Part 4 ("From Molecules to Ecosystems") concerns the impact of Darwinism on the manner of conceiving the great questionings of biology, following a classic but eloquent design – that of the levels of integration. We therefore pass from the molecular level to the most integrated level – the ecosystem. This part also discusses the relations that are maintained between medicine and Darwinian thought.

Part 5, "Exported Darwinism" is designed to again show the fecundity of Darwinism, but – and this is an important "but" – outside of its initial and obvious field of application, the evolution of entities within biology. The human sciences, ethics, and the cognitive sciences are of principal concern here. In a dedicated report, we wanted to give a thoroughly developed survey of a flourishing field of research that also exemplifies this process of exportation – that of the field of evolutionary psychology.

To finish, Part 6, "About Anti-Darwinism" discusses the new creationist offensive, principally launched by the Intelligent Design movement. Education being the chief target of creationists of all kinds, a chapter wonders about the ways in which one can discuss the very difficult theory of evolution within the realm of the life sciences, of which the mechanisms, the reasonings, and the explanatory schemes are not only abstract, but go against the grain of the most spontaneous of our perceptions and interpretations of the real world.

If it is important to conclude by clarifying that the scientific and cultural aim of this panorama is not to place Darwin on a pedestal, and still less to pretend that Darwinian dynamics have an answer to all scientific questioning, it is also important to note that we hope the reader will find in these pages the opportunity to critically reflect on a rich theory, on the methodological rigour that presides in its extensions and exportations, on the necessity to measure its advantages and also its limits. The multiple forms of Darwinism are, in these matters, a formidable field of play: may the reader share our enthusiasm for them and be tempted to explore their immense richness.[5]

[5] Translated into english by Adam Hocker. More generally the editors are grateful to Elizabeth Vitanza for having translated many chapters into english, to Adam Hocker for english language revision and translation of some chapters, and to the Editions Matériologiques (Paris) for graciously allowing us to translate into english the majority of the chapters from the book Les Mondes Darwiniens, which was initially published in 2009 an then republished, updated and enhanced, in 2011.

Thomas Heams is assistant professor in animal functional Genomics in AgroParisTech, the Paris *Institute for life, food, and environmental sciences*, and is a researcher at INRA the french *National Institute of Agricultural Research*, in the animal genetics division. His teaching and research activities relate to animal evolutionary biology, biotechnologies, human/animal relationships, and the critical history of scientific ideas.

He has been an advisor for the French Parliament Office for science and technology, and has supervised several translations of scientific essays into french. He is a board member of the Editions Matériologiques.

Philippe Huneman First trained in mathematics and then in philosophy, Philippe Huneman is Research Director (eq. Full Professor) at the Institut d'Histoire et de Philosophie des Sciences et des Techniques (CNRS/Paris I Sorbonne). After having studied the constitution of the concept of organism in modern biology in relation with Kant's theory of purposiveness (*Métaphysique et biologie*, Paris: Kimé 2008 and many papers in philosophy journals and books), he turned to the philosophy of evolutionary biology and ecology. In this field he edited several books (*From groups to individuals,* on individuality with F. Bouchard (MIT Press 2013); on functions ("Synthese Library", 2013), and published papers on the relationships between natural selection and causation, on the roles of organism in evolution, as well as the status of development in recent evolutionary theory, and on the computational conception of emergence in general, as well as issues in modeling and simulation. http://www-ihpst.univ-paris1.fr/5,philippe_huneman.html

Guillaume Lecointre Guillaume Lecointre, Scientist (systematist), teacher, Professor at the Muséum National d'Histoire Naturelle, Paris. Head of the Research Department "Systématique et Evolution" (250 persons in the department, two units of research). Head of a research team in the unit of research "UMR 7205 ISYEB" (CNRS-MNHN-UPMC-EPHE) "Institut de Systématique, Evolution et Biodiversité" (Direction: Pr. Philippe Grandcolas). Applied and theoretical systematics, phylogenetics, systematic ichtyology, antarctic ichtyology. 103 professional publications, 11 books, 400 papers of science popularization.). Double Laureate of the Société Zoologique de France (French zoological society: Prix Charles Bocquet (2006), Prix Gadeau de Kerville, 1996), National Laureate 2009 of the "Comité Laïcité République", Laureate 2012 de "Union Rationaliste" (Rationalist Union).

Marc Silberstein Independent scholar, French publisher (sciences, history and philosophy of sciences) Editions Matériologiques, Paris, www.materiologiques.com.

He is co-editor, with P. Huneman, G. Lambert, of Classification, disease and evidence. *New Essays in the Philosophy of Medecine* (Springer, 2014).

Part I
Concepts: Processes

Chapter 2
Variation

Thomas Heams

Abstract Understanding the origins of biological diversity is one of the main challenge for biologists. But in evolutionary biology, variation is also a starting point: natural selection can generate evolution because populations are made of non-identical individuals, transmitting different genetic combinations to offsprings. The sources of these heritable variations are to be found in the structure of DNA, the molecule of heredity, which combines feature of stability with a potential for mutability at different scales. In addition, epigenetic mechanisms can provide another source of heritable variations and evolvability.

Variation lies at the core of Darwinian thought and the concept of natural selection.[1] The rehabilitation of variation as a biological parameter is one of the major reason why Charles Darwin's ideas remain so modern.[2] For the English naturalist, though this modernity does not consist of having postulated the evolution of species. Others preceded Darwin, most notably Jean-Baptiste Lamarck, who formulated this hypothesis in 1809 (laying the foundations for it in 1802); Lamarck also suggested a largely discredited mechanism for evolution, the effect of use and non-use associated with the heredity of acquired traits. Far from being a stubborn *idée reçue*, this mechanism was of interest to Darwin—it is even the subject of one of his main works: *The Variation of Animals and Plants under Domestication 1868* –, but he had also proposed another major mechanism, natural selection (simultaneously with Wallace) that he considered as complementary, and which proved to have the most powerful impact on the explanation of evolution, all the more than heredity of acquired characters would in the same time be largely disproved. Within the hereditary mechanism of acquired traits[3], the appearance of a variation is the product

[1] See Huneman, Chap. 4, this volume.

[2] On this crucial question, see Charbonnat.

[3] See Heams, "Heredity", Chap. 3, this volume.

T. Heams (✉)
INRA, UMR 1313, Génétique Animale et Biologie Intégrative,
Domaine de Vilvert, 78352 Jouy-en-Josas cedex, France

Département Sciences de la Vie et Santé, AgroParisTech,
16 rue Claude Bernard, 75231 Paris cedex 05, France
e-mail: thomas.heams@agroparistech.fr

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of a force: the giraffe stretches its neck *in order to* be able to reach the highest leaves, and, always according to this mechanism, this variation—provided that it was carried by both parents and under certain age conditions—can be transmitted to offspring. In this sense, Lamarckism, although it is a type of evolutionism, remains limited to a universe whose basic principle is stability. There *must be* a force that creates variety. Without one, there is no urgency and no evolution. In Darwin's proposed mechanism of natural selection, nature carries out a selection from the variations that appear *spontaneously.* This distinction appears to be nuance at first glance, yet it is in fact a radical shift in perspective. The possibility for nature to always create variations yields a vision of a dynamic world in a permanent state of transformation, calling into question the notion of a fixed universe. The transformation of the world is intrinsically linked to the existence of variation rather than being the occasional consequence of favorable circumstances. One can keep a wondering why Darwin was the among the very first to suggest this new perspective. Global and the individual factors likely have produced this foundational moment in modern biology. For Darwin, the intersection of the Enlightenment's far-reaching influence as a freedom from a previously fixed world, profound changes in Western social structures throughout the nineteenth century, and his random luck as an observer with unequaled curiosity led to his studies of animal husbandry in England as well as the finches in the Galapagos Islands. Even if it is clear that the idea had been ripened for the picking by earlier research, such as the works Alfred Russel Wallace was above to publish as soon as 1858.

1 Which Variations Can Be Transmitted via Evolutionary Pressures at Play?

Yet what, physically, are these inheritable variations Darwin referred to without having the experimental means to discover them? The issue is more complex than it first appears: in a population, in a living organism, in an organ, at all levels, everything varies all the time (Hallgrımsson and Hall 2005). This variability (the ability to vary) and this variety (this result of variability) are physiological and anatomical: there are around 250 types of cells in a mammal such as man. These cells are also temporal: despite the feeling our permanence, which founds our identity and our individuality, nearly every cell in our bodies is regenerated roughly every 15 years leaving our bodies are nearly wholly changed; our most essential cells are much younger than we are. If we move to the molecular or atomic scale, the exchanges are even more dynamic since even the perennial macroscopic structures like bones are periodically renewed in their totality. These constant exchanges between life's entities, and which constitute metabolism, are the very subject of biological science in the broadest sense.

In the Darwinian paradigm that concerns us here, the goal is thus to reformulate the question "what varies?" into "what are the variations that can be transmitted by the evolutionary pressures at play?". This is a drastic restriction of the first question,

but as we shall see, it still remains incredibly vast. Darwin and his contemporaries observed visual variations of traits. The mode by which these traits were transmitted remained a mystery, and when he attempted to define it, Darwin suggested hypotheses that ultimately were false. Far from diminishing the merits of natural selection formulated in *On the Origin of Species* using incomparably rich data, however, natural selection is all the more commendable for having been suggested when its physical evidence was inaccessible. Rapid development of genetics at the beginning of the twentieth century followed the rediscovery of Gregor Mendel's work (already three decades old) on the transmission of material determinants, or *genes*, from generation to generation. "Material determinants" means that, on one hand, these are physical entities, and that, on the other, each one theoretically has a link with an elementary observable trait that it "determines". Evolutionary biology in the twentieth century will use these two fields of research: finding modes of transmission and finding the link between these entities and the corresponding trait.

The historical periods of understanding transmission have been the following: over the course of the first half of the twentieth century, genes were progressively localized in the cell's nucleus, then physically on the DNA molecule, present in each of our cells. When James Watson and Francis Crick uncovered in DNA's structure in 1953, the completed the discovery by describing DNA as a linkage of small units of just four types (adenosine, guanosine, cytidine, thymidine) referred to by their first letter (A, G, C and T), in a long pearl-necklace pattern so that each chain comprises a sequence unique to each individual (Watson and Crick 1953, with Rosalind Franklin). Furthermore, this molecule has two strands: when a cell divides, in can thus transmit two identical batches of DNA to its daughter cells. This is as true of a bacterial division as it is of a liver cell. DNA led, therefore, to a broad understanding of how these determines are transmitted. In addition, many geneticists had not waited for this structural discovery to demonstrate that certain agents like chemicals or X-rays could cause changes in certain traits. Watson, Crick & Franklin's discovery finally allowed them to see concretely the mechanism by which what were then referred to as mutagenic agents could have an influence on genes: they did so by modifying the DNA sequence at certain crucial points at a certain point in time. Now called *mutations*, these are exactly the variations that can be affected by natural selection since they are both linked to a trait and transmissible. It is also to these broadly defined mutations that we will now turn in greater detail.

2 How Do Mutations Appear?

Nevertheless, if only X-rays or chemical products could cause mutations, then that would still not explain their occurrence in nature. Here, molecular biology provides the essential elements for understanding how these two things could themselves spontaneously appear. The main reason, the one that is universal in the living world, is that they are duplication errors. This is possible because the cell duplicates its

genome (all of its DNA) prior to cell division. This duplication occurs due to a battery of enzymes that will, base after base, synthesize the copy in question. In humans there are several billion base pairs to faithfully duplicate. It is reasonable to imagine that even one extremely reliable enzyme that will, through biological evolution, have progressively developed to photocopy will never be *totally* reliable. Every few thousand or even hundred thousand bases depending on the species, this enzyme will occasionally make errors, and thus create mutations. These mutations will, moreover, have another particularity that squares perfectly with what Darwin intuited and what was observed in the first experiments carried out in experimental genetics: their appearance, and thus their position on DNA, are random. The DNA copy will very closely resemble the matrix, but it will never be exactly the same. This is the key to genetic mutations, which we can look at with the same perspective as Darwin had on the organisms he observed: the finesse and sophistication of this copy's molecular mechanisms begs the question of how variations do *not* appear more often rather than how they appear at all! The capacity for creating variation is intrinsic to the mechanisms at work and it is thus not necessary *a priori* to search for a specific mechanism that generates variation; it is even less necessary to seek a force that will have this effect.

At this point, this return to Darwin requires an explanation of the link between genes and traits. Molecular biology demonstrated it: each sequence of the gene codes for a specific protein according to a (quasi) universal correspondence called the genetic code. Modifying one sequence of DNA can thus lead to a modification of the corresponding protein sequence and then of the trait in question. The classic example is the following: a simple -well known- mutation of the genetic sequence of hemoglobin can cause a single amino acid to change, which is enough to modify the hemoglobin's folds and affect its ability to carry oxygen. Individuals who carry this mutation, especially if they inherit it from both parents (not just one) can present a major respiratory pathology. The link is thus established between the variations Darwin observed and those that geneticists observe in DNA. Natural selection will act upon traits, also called phenotypes, and favor the corresponding genotypes (groups of genes) to the detriment of others. It has been clear for a long time, however, that the "one gene/one protein" relationship is much more complex than the one I have summarized here. One sequence may be read more or less partially, giving rise to different proteins, and thus to a supplementary variability. A gene can also act upon several traits, a phenomenon called "pleiotropy". When mutations intervene in coding sequences and are not counter-selected, they create different copies of the gene involved. These copies can coexist in a population and may potentially have different corresponding proteins. These copies are called *alleles*. A given gene will be a homozygote it the paternal allele is identical to the maternal allele; it will be a heterozygote if they differ. Population genetics is the discipline that studies populations from the angle of allelic frequencies of certain genes under the effect of evolutionary pressures: mutation, selection, migrations or genetic drift (random variation of an allelic frequency best seen in small populations).[4]

[4] See Huneman, Chap. 4, this volume.