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General Introduction

Unlike many natural philosophers of the seventeenth century, whose work bridged what we now call science and philosophy, most twentieth-century philosophers of science did not undertake serious work in what we would now call science. Often enough, they wrote in reaction to earlier writings of scientists and philosophers of science, drawing on general background knowledge. Although the theories and analyses they produced were often fascinating, this narrow way of working put them at risk of making poor contact with the phenomena of concern to scientists. Some philosophical projects fell victim to this risk, including some attempts to construct general theories of scientific method, to develop criteria for distinguishing living from nonliving entities, and to specify the structure of major biological theories. Often enough, there turned out to be more things in heaven and earth than were dreamt of in our philosophies (Shakespeare, *Hamlet*, I. v). Philosophy, including philosophy of science, should begin with wonder at the phenomena that require understanding.

The development of the philosophy of biology in the last thirty years or so has been salutary in this regard as it has become ever more involved with biological phenomena. Like many contemporary philosophers of biology, I maintain that the phenomena of biology, and its history, are more far more complex – and confusing – than traditional philosophers imagined. Thus, a central theme of the essays that follow is that philosophy of biology must be learned, taught, and thought about by working intensely with "real biology" and serious history of "real biology."

There is, however, a dialectically counterpoised point. The phenomena that biologists study are extremely complex. Valuable insights about complex systems can be gained by working with what scientific modelers sometimes call "toy models." Because philosophers often work with conceptual models and have developed critical tools for this purpose, their training helps them raise well-thought-out questions about the use of models in biology and about how well those models bear on biological knowledge claims. In short, philosophers who are well informed about biology can hope to work closely with biologists in dealing with the various complexities that infect biological work. Philosophical models and the tools of philosophical criticism can help in "locating" problems within larger intellectual contexts, detecting hidden presuppositions and categorizing the advantages or disadvantages of various instruments or model organisms in pursuing certain aims or particular problems. Philosophers can help dissect problems so that they can be rethought in new terms, and they can analyze various ways in which complex units might act as causally integrated wholes. In short, although history and philosophy of biology cannot be done without close contact with biology, historians and philosophers who pay close attention to biology can (at least sometimes) shed light not only on the history and development of biology but also on useful ways of coping with biological problems.

This book is organized in four parts and brings together eleven interrelated essays, written during the last two decades. As such, it does not put forward a neatly unified point of view for it reflects some of the differences of viewpoint among biological disciplines and some of the major developments in biology, which has undergone enormous changes in the last two decades. Nonetheless, the volume is surprisingly unified. It builds on my enduring interest in three related topics: the historical development of work in evolution, genetics, and development; the epistemological issues raised by the interactions among these (and other) disciplines; and the difficulty in achieving conceptual unification of the accounts of the phenomena studied in these biological domains and in biologists' accounts of organisms more generally. It builds to a climax in the concluding chapter, which examines aspects of the ongoing reconception of the ways in which animals are put together thanks to the new integration of development, evolution, and genetics now under way in evolutionary developmental biology.

Part I contains two chapters about general methodological issues: the use of "model organisms" (a term of art of the late twentieth century) in biology and the methodological importance (and difficulty) of "interdisciplinary unification" within biology. Both chapters were written for symposia and address the papers presented at those symposia, but their central arguments can be easily understood without examining the papers in question. These two chapters help set up one of the most fascinating dialectics in biology: the dialectic between the particularity of findings and contingency of organismal traits (which are both reasons for worrying about the feasibility of unification in biology) and the importance of the search for general unification within biology. For those with philosophical interests, one of the main thrusts of this book is that whatever we make of the degree of unification achieved in biology, it is not achieved by establishing a set of general biological laws under which explanations can be subsumed. Organisms embed too much history within them (not only their evolutionary histories but also their individual ontogenies!) for them to fall under laws modeled on those of physics. This illustrates one of the continuing themes of the book, introduced in Part I.

The other three parts of the book focus on evolution, genetics, and development, paying particular attention to the interactions among these disciplines. Because each section has its own introduction, it is not necessary to elaborate upon them here.

Most of the chapters were written for specific occasions. The thematic unity of the book rests, in part, on resistance to excessive reductionism and on a commitment to what might be called "contextualism" – that is, to the importance of understanding the multiple contexts within which knowledge claims, including those of biology, are put forward and the bearing of those contexts on the interpretation of the claims put forward by biologists. Accordingly, most chapters pay close attention to aspects of the historical settings of the biological problems they examine. I seek to help the reader understand how the available biological knowledge and instruments of research yielded challenges to the then-prevalent conceptual tools and theories of the biologists and how, if at all, such difficulties were – or might have been – resolved in context. By returning repeatedly to the interactions among biological disciplines and to the available investigative tools, I reinforce the importance of issues raised by divergences among disciplines. I also locate some reasons for the failure of reductionist programs to provide satisfactory explanations of biological findings by restricting attention to a single level or biological discipline. Throughout the book, I maintain that biology is built on cross-disciplinary interactions that cover micro- to macro evolution and molecules to whole organisms – not just because of the organization of the disciplines themselves but also because organisms, which are thoroughly historical entities, are built via interactions across ontological levels, with both upward and downward causation.

It is in good part thanks to the influence of Marjorie Grene that I have come to recognize the multilayered and multileveled complexity of biological phenomena and the sciences that deal with them and the importance of placing problems – and scientific work – in a proper historical context. If these underlying attitudes are correct, we will not understand the ongoing transformations of biology until we appreciate both *what issues were at stake at particular junctures* and *how difficult it is to match up the concepts employed by scientists working in different disciplines or in different temporal and social settings*.[1] Thus, among the commitments that I hope the reader will take away from this book are the following:

- To understand scientific work properly, one must locate it in its proper intellectual, scientific, and social contexts.
- No single strategy can adequately describe – or prescribe – sound scientific method.
- Reductionism (itself multifaceted and variable in content and style) is one of the most productive organizing (or heuristic) principles for research in biology.
- But, the heuristic power of reductionism often leads scientists to miss important features of the context and organization of biological entities.
- Accordingly, neither the ontology of living beings nor the epistemological difficulties raised by the scientific study of organisms are revealed by focusing exclusively on reductionist strategies in biology or the progress achieved by use of those strategies.
- The clash of disciplinary insights – which include commitments to particular instruments and methods, not just commitments to theoretical positions – is often a key factor in major advances in biology.
- For this reason, cooperative and competitive investigations across disciplines are often essential for the solution of biological problems.
- Correspondingly, understanding of investigations that cross disciplinary boundaries is crucial for understanding how many biological problems are solved.
- The tools of cooperative investigation include the more-or-less philosophical tools involved in reconciling conceptual conflicts – reconciliation accomplished in part by conceptual analysis, in part by empirical and experimental research.

The chapters of this book, written for diverse audiences, highlight the importance of diverse perspectives and bring to bear insights drawn from different sources. The introductions to the four sections help set the chapters into context and provide some guidance about background presuppositions. Accordingly, gentle reader, I hope that you will forgive occasional small overlaps between the chapters and find them instructive rather than tedious.

[1] For some of my more philosophical papers elaborating on these matters, see Burian 1992, 2000, 2001, 2002; Burian and Trout 1995.

And I hope that you will find and correct the errors and oversights that, no doubt, abound in this book.

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I

Methodological Issues

The two chapters in this section, both published in 1993, illustrate the importance of the meetings of the International Society for History, Philosophy, and Social Studies of Biology (ISHPSSB) as a vehicle for interdisciplinary communication. Chapter 2 was first presented in 1991 at an ISHPSSB symposium, which Muriel Lederman and I co-organized, on "the right organism for the job." The papers from the symposium were published as a special section of the *Journal of the History of Biology* (Lederman and Burian 1993). The symposium was inspired in part by an earlier symposium organized by Adele Clarke and Joan Fujimura, held at the 1989 ISHPSSB meeting and later expanded into a book titled *The Right Tools for the Job* (Clarke and Fujimura 1992). Chapter 3 was originally presented at another 1989 ISHPSSB symposium on the importance and difficulty of integration and unification in the biological sciences. The methodological and epistemological issues at the center of all three symposia received wide attention.[1]

The symposium on model organisms focused on a distinctively biological topic in scientific methodology.[2] Experimental work often requires development of an experimental system (Rheinberger 1995, 1997, 1998). In biology, it often depends as well on the domestication and development of an organism especially suited to the problems at hand. For example, when biologists

[1] The electronic version of the Science Citation Index (including the Humanities and Social Science indexes) contains about three hundred citations to the published versions of the three symposia mentioned in this paragraph, including citations to the individual papers as well as the symposia. About two-thirds of the citations are to *The Right Tools for the Job* or its individual chapters.

[2] The literature on model organisms, already large before our symposium, has grown enormously in the last decade, partly because granting agencies have dedicated considerable funds to a small group of specific model organisms. I list here a sampling of recent references of interest to readers of this book: Ankeny 1997; Bolker 1995; Bolker and Raff 1997; Bolker (moderator) et al. 1998; Buntin 1997; Burian 1996; Davis 2000; Dooley and Zon 2000; Gest 1995; Kohler 1994; Logan 1999, 2001; Schneider 2000; Strange 2000; Wayne and Staves 1996.

were limited mainly to breeding experiments and conventional forms of microscopy in studying genes, the relationship of genes to chromosomes could be studied in detail only in organisms with a small number of chromosomes that were easily visualized in standard microscopes and relatively easy to distinguish from one another. In contrast, entirely different requirements had to be met by organisms especially suited to the study of respiratory physiology or to the study of cell lineages (i.e., the developmental history of lines of cells derived from a particular embryonic cell). Thus, starting in the nineteenth century, certain organisms came to be used as models in certain studies. Only later was the use of such models amplified in a way that led to the creation of "model organisms" intended to serve a series of rather general purposes.

Arguably, organisms that can be domesticated in the laboratory represent a biased sample of organisms, with distinctive properties that contribute to rapid turnover, relatively simple ontogenies, and easy standardization – properties that are not characteristic of organisms in general (Bolker 1995; Bolker and Raff 1996; Bolker (moderator) et al. 1998). Thus, on the one hand, to gain access to particular properties of organisms or processes of interest within and between organisms, it is often necessary in practice to use "exceptional" organisms whose exceptional traits make it feasible to study the properties or processes in question. On the other hand, the exceptional character of such model organisms risks fostering systematic bias and puts the generality of the results thus obtained in doubt. The papers in the symposium dealt with these issues and addressed, specifically, historical and methodological issues associated with the use as models of bacterial viruses (Summers 1993), chlamydomonas (a one-celled green alga used, among other things, in the study of photosynthesis) (Zallen 1993), frogs (Holmes 1993), *Drosophila* (Kohler 1993), plant viruses (Lederman and Tolin 1993), and rats (Clause 1993). Chapter 2 is both a general summary of issues raised in the symposium and my attempt to frame some of the key methodological issues raised in those papers.

Chapter 3 was published as part of a symposium on integration in biology (Ruse and Burian 1993). It begins in reaction to van der Steen's criticism of the ideal of unification of the biological sciences and of misapplications of that ideal (van der Steen 1993). The chapter then expands on some of the issues briefly touched on in Chapter 2 by use of a case study of work in the early 1940s leading up to the one-gene – one-enzyme hypothesis. In particular, I explore the importance of the contingencies that arise from the availability of particular tools and techniques and of bringing the experimental and conceptual tools of different disciplines to bear on common or overlapping problems. In the process, I argue that the ideals of resolving conflicting claims and, sometimes, of unifying the conflicting conceptual apparatus of different disciplines serve as important second-order ideals for the development of (biological) sciences. At the same time, I argue that these are weak ideals, for they cannot give specific guidance about the pathway toward resolution or unification. Thus, the ideal does not provide guidance as to whether one or another discipline provides the appropriate basis for unification. Thus, the ideal of unification can be dissociated from the drive toward reduction – even sophisticated weak versions of reduction such as Schaffner's General Reduction–Replacement Model, presented at the same symposium (Schaffner 1993a) and in much greater detail in Schaffner (1993b).

The pairing of these two chapters provides a basis for key arguments about the centrality of "local knowledge"; for example, the partial, open-ended knowledge localized in particular disciplines or based on particular techniques. The contingency of evolution and the openness of the knowledge situation of ongoing scientific investigations both contribute to this conclusion. These themes return in subsequent chapters of the book.

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2

How the Choice of Experimental Organism Matters

Epistemological Reflections on an Aspect of Biological Practice[1]

> Unless we recognize our innate biases in animal model choice, we limit our potential as experimenters. Two biases seem common from my observations. First is the anthropomorphism that we all seem to get from the monkeys in zoos and circuses, coming as it does long before we aspire to be scientists. Second is for the animal or animals with which we worked during our early days in our fields. Both of these are easy to understand and forgivable. What has neither of these saving attributes is our unwillingness to consider the entire biologic kingdom as a source of possible models of one or another human functions, normal or diseased.[2]

The value of an organism[3] as an experimental tool, or in field studies, depends not only on various features of the organism[4] but also on the problems to be addressed and the available experimental and field techniques. Indeed,

1 Published in *Journal of the History of Biology* 26 (2) (Summer 1993): 351–67. © 1993 Kluwer Academic Publishers. Reprinted with kind permission of Kluwer Academic Publishers. This was the concluding paper of a special section in the same issue of the journal on "The right organism for the job," eds. M. Lederman and R. M. Burian, 233–367. The section contains papers by Richard M. Burian, Bonnie Tocher Clause, Frederic L. Holmes, Robert E. Kohler, Muriel Lederman, and Sue Tolin, William C. Summers, and Doris T. Zallen. I am grateful to Marjorie Grene, Muriel Lederman, Anne McNabb, Doris Zallen, and a *JHB* referee for their helpful critical readings of a late draft of this chapter.

2 Prichard (1976, p. 172); used as a chapter epigraph at p. 24 of Committee on Models for Biomedical Research 1985.

3 I take "organism" in a broad sense here, including such artificial "organisms" as somatic cell lineages in tissue culture. Such biological "material" plays much the same role as an organism for the purposes of this chapter.

4 This seemingly essentialist *façon de parler* ("the organism") is for convenience only. One of the most important features of "an" organism (i.e., conspecifics, or organisms belonging to a particular strain, perhaps an especially prepared laboratory strain) may be the variability "it" exhibits. Nor is variability always undesirable. Consider, for example, genetic studies of the norm of variation (i.e., the range of phenotypes produced by a given genotype under various circumstances). As this illustration shows, the use or construction of a specially prepared laboratory strain aims