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Bioknowledge with Burian

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Review of Richard M. Burian's *The Epistemology of Development, Evolution, and Genetics: Selected Essays*. New York: Cambridge University Press, 2005

Introduction

Like a number of leading contemporary, senior players in the philosophy of biology – Philip Kitcher and Elliott Sober come readily to mind – Richard Burian began his career focused on general issues in the philosophy of science. In Burian's case, these were issues about the unity of science, conceptual change in science, the nature of scientific discovery, and inter-theoretical explanation. Fortunately for the community at the intersection of biology and philosophy, Burian shifted his attention from the late 1970s increasingly to the biological sciences, making important contributions to something close to the full range of topics that now constitute the field: to understanding central concepts in evolutionary theory, such as adaptation and the levels of selection; to our grasp of the significance of the molecular revolution in the biological sciences; to the application of evolutionary thought to the human domain; and to genetics and development, and the relationship between them. Yet the philosophy of biology has never been solely about writing or giving papers for Burian, and he has been one of the field's most active community builders, helping to found the International Society for the History, Philosophy, and Social Studies of Biology in the early 1980s (ISH to its friends, especially its friends who struggle even to say "Ishkabibble"), and an organizer and leading participant in many symposia, colloquia, and conferences that have created spaces for many others in the field to fill. A trademark of Burian's own written work, manifest also in his community-building efforts, has been its integration of historical and philosophical themes.

The 11 substantive essays in this collection, four of them published here for the first time, provide a representative sampling of what Burian has to say about four themes: the epistemology of biological practices, such as the use of model organisms; evolution and its place in biology; genes, genetics and molecular biology; and developmental biology, particularly its renaissance in the past 10 years. In many ways the first theme, construed broadly, provides a kind of umbrella for the volume as a whole in that the essays it contains are all concerned, in one way or another, with how it is that biologists go about earning their keep, and the philosophical fallout that their activities and practices generate. Thus, given a correspondingly broad view of epistemology, the title of the volume is apt insofar as Burian is here concerned first and foremost with bioknowledge – its basis, limitations, and absence – anchored in the ongoing struggles both within and between the sub- and cross-disciplinary fields studying development, genetics, and evolution.

This collection will be an important acquisition for anyone working in the history or philosophy of biology, and for biologists who have wondered about either the broader context of their own specialization or about dispute and debates in some areas of biological science beyond that specialization. Many will be familiar with some of the papers reprinted here. Only a small number of these papers, however, have appeared in journals (two in *The Journal of the History of Biology*, and one in *Biology and Philosophy*), and several of the previous edited volumes housing others have perhaps not been as widely read as one might have hoped. For those beyond the primary audience of historians and philosophers of biology, the collection may be of more restricted use or interest, containing as it does only one paper published since 1993 (in 1997, in fact), with most papers heavy on either the historical or the biological details regarding the issues they discuss. Although each paper has been updated, nearly all of these updates are minor and serve chiefly to set the context for the paper, and so don't help out in this regard; much the same could be said of the brief introductions to the four sections of the book. Burian has taken the opportunity to publish material that had previously been presented only at symposia and conferences, sometimes stretching back over 20 years ago, and for my part at least I wished for a little more orientation towards discussion of the many contemporary issues that have taken center-stage in the field only in the last decade: for example, genetics and developmental systems theory, the major transitions in evolution and the levels of selection, post-genomic research, and reassessments of the evolutionary synthesis. There are glancing discussions of some of these – the first and fourth – but not as much reflecting the recent literature as one might like. Even with that caveat and caution, both relatively uninitiated readers and those familiar with Burian's published work will find the unpublished papers based on talks he has given, especially those that focus on the exciting findings in contemporary evolutionary developmental biology, providing a kind of useful entry point into some recent literature of broad philosophical significance.

Knowledge and ignorance in the biological sciences

A pair of issues concerning bioknowledge that Burian shows keen sensitivity to in a number of these essays is the limit of our knowledge, and cases where claims to knowledge outstrip the evidential basis for those claims. An important part of knowledge is knowing when you don't know. While someone with more post-modern panache might say that "Knowledge is ignorance", we can avoid both the excitement and the confusion that such a claim generates by sticking with my more mundane expression of this point: knowledge is sometimes knowledge of ignorance. Scientists are sometimes blinded to this fact. This is both for institutional reasons (who gets tenure for proudly pronouncing one's ignorance? In what field is the Journal of Non-Results published?) and because scientists are human, subject to the same excesses and distortions of the moment that all epistemic agents are subject to. Two examples, drawn from Burian's discussion of development in these pages, help to illustrate what I mean, and to convey some of the richness of Burian's own discussion.

There is a paradox of sorts about ontogenetic development, what Griesemer (2000) has called "the paradox of development" and that Burian here calls "Lillie's Paradox". It is this: given that, to a close approximation, all cells that a metazoan possesses share the same nuclear DNA, and so the same genes, how can an appeal to genetic inheritance explain organismal development? Burian names the paradox after Frank Rattray Lillie, who articulated an early version of it in 1927; as Burian makes clear in his discussion, versions of this paradox stretch back into the late 19th-century, at least to Weismann's *The Germ-Plasm* (1893). The paradox is located in the struggle between preformationist and epigenetic views of development and evolution, and epitomized the related struggle between geneticists and embryologists from that time. But that way of conceptualizing the key issue of how it is that ontogenetic development takes place presupposes what Burian, following Boris Ephrussi, calls "the geographical distinction" between nucleus and cytoplasm. And, as Burian continues, that distinction "came to be an obstacle to an integrated understanding of heredity and development, an obstacle that had to be overcome before there could be any real hope of breaking down the conceptual barriers between genetics and developmental biology" (p. 186). As genetics emerged as a distinct field in the first decades of the 20th-century, many leading geneticists were gripped by the idea that geographically segregated entities, genes, in some sense contained the whole organism, serving collectively as (to leap ahead to metaphors that came into play in the 1940s and 1950s) a blueprint or program for organismic development. As Jacob summarizes it near the outset of his *The Logic of Life* (1973: 2), "[i]n the chromosomes received from its parents, each egg therefore contains its entire future: the stages of its development, the shape and the properties of the living being which will emerge. The organism thus becomes the realization of a *programme* prescribed by its heredity." Such a view was maintained within both Mendelian and molecular genetics throughout much of the 20th-century. This was so despite a general recognition of the paradox of development, and despite counter-indicating experimental findings with organisms (e.g., ciliated protozoa in the 1940s and 50s) other than those that came to serve as model organisms within the core of those research paradigms.

Burian traces this history through to a pair of publications by Ephrussi and by the ciliate biologist Nanney in 1958 that played an important role in the articulation of the distinction between coding and regulatory genes made by Jacob and Monod in 1961a,b. Part of Nanney's message is that a distinction more relevant for understanding development is that between encoded information (that is often but not always encoded in nuclear structures, including genes) and systems that control the expression of that encoded information (that are often but not always extra-nuclear). One might see in Nanney's work, both here and elsewhere, just the kind of pluralistic, locally-based knowledge claims that Burian thinks lie at the heart of the biological sciences, and that express Burian's own normative views of what we could do with more of in those sciences. A recognition of the limits of knowledge lead to conceptual innovation, methodological diversity, and a preparedness to entertain unorthodox and often marginalized views. That is scientific progress of sorts, and I suspect that Burian himself would think that when it fails to be the statistical norm in the biological sciences, those sciences are the worse for it.

A second example emerges in the final pair of papers in the volume and concerns relatively recent work on homeobox genes. The homeobox is a sequence of DNA, usually 180 nucleotides in length that encodes 60 amino acids, which in turn serve as a transcription factor (called the homeodomain) regulating the formation of proteins. Homeobox genes play a key role in the developmental cascade that structures an organism's body development, and perhaps the most striking finding is how widely shared these genes are amongst organisms that are phylogenetically very distant. There are homologues between the homeobox genes that structure anterior–posterior development in the fly and the mouse, to take the example that is most often discussed. Walter Gehring, who has done some of the fundamental work on homeobox genes, based on the *ey* (for eyeless) gene in *Drosophila* and its homologues *Sey* (small eye) in mice and *Aniradia* (lack of iris) in human beings, is well-known for his claim that, in light of their wide phylogenetic distribution and the result of genetic engineering studies that shifted where *ey* (for example) is expressed, homeobox genes are "master genes" for development (Gehring 1998).

After recounting the historically and biologically relevant details of the case of homeobox genes in the first of this pair of papers, "On Conflicts between Genetic and Developmental Viewpoints – and Their Attempted Resolution in Molecular Biology", Burian challenges this interpretation of the findings, on two grounds. The first is that it reinforces "the metaphor of the genome as a program that contains the entire organism *in potentia*" (p. 225), a metaphor that Burian views as misleading. The second is more interesting in that such a view obscures a real issue about the nature of homology, ignoring both its status as a matter of degree and the distinction between the homology of *products* and that of the *processes* of evolution. (Burian makes more of this distinction in the final essay "Reconceiving Animals and Their Evolution".) Burian takes "one of the morals of this story to be that we do not yet know what is required for a deep improvement of the explanatory apparatus with which to explain many aspects of organismic development" (p. 228); talk of "master genes" obscures our ignorance here.

Contextualism and Bioknowledge I: Heterogeneity and Natural Kinds

Burian's plea for an acknowledgement of our ignorance, and the related call for a recognition of the limits of particular research traditions and disciplines, should not be read as a kind of skepticism about bioknowledge. Rather, Burian develops such a view as part of an overarching anti-reductionist, contextualist epistemology of scientific knowledge, identifying it, in his short introductory essay, as providing the "thematic unity of the book" (p. 3). It might be worth trying to tease out what such an epistemology of bioknowledge amounts to, since one might worry that it simply recognizes disciplinary perspectives as partial, the knowledge they generate as incomplete, and a multiplicity of approaches as Good Things. What, more specifically, is Burian's positive view of the epistemology of biological knowledge?

One positive theme here is the significance of a distinction between the objects of physics and those of biology, a distinction that the physicist Elsasser emphasized some 40 years ago in *Atom and Organism* (1966). Put crudely, if you've seen one electron, you've seen them all; if you've seen one instance of *any* biological entity, you've just started down the path to bioknowledge. Crucial to biological knowledge is recognition of what I have elsewhere (Wilson 2005: 52) called the *intrinsic heterogeneity of the living world* and a corresponding view of biological kinds. Let me spell out this view a little and say something about its relationship to parts of Burian's discussion.

Biological kinds, of their nature, subsume entities that are different from each other in ways that are important for their being instances of those kinds. On traditional views of natural kinds, differences between instances that fall under the same kind are abstracted away from; such differences are the result of properties or circumstances that are not important to the kind. Thus, one way to think about members of any natural kind are as sharing a set of *essential properties*, each of which is necessary and together which are sufficient for being instances of that kind. Perhaps being composed of molecules of sodium chloride is a simple example of such an essential property for the natural kind salt. Any instance of salt has lots of other properties, such as relating to certain other chemical compounds (e.g., water) in certain ways, or having a certain mass, but these are non-essential to its being an instance of salt: they are to be bracketed out or ignored when we consider something *as salt*.

Perhaps this kind of essentialist view of natural kinds is right about some kinds of nature – those of physics and chemistry, for example. That would reflect the idea that any one instance of those kinds is as good as any other, that their interchangeability is not simply allowed but *required* for the sort of generalizations that one makes in those sciences. But this is at best only poorly approximated in the biological sciences, and in many ways such views are problematic when applied to at least some biological kinds. Consider essentialism about a putative biological kind, such as *Canis familiaris*, the domestic dog. There is no set of intrinsic properties, each necessary and together sufficient, for being a dog. Perhaps the properties we need to consider here are *historical*, such as the phylogenetic relation of descent, or relational in other ways, defined in terms of notions such as interbreeding and reproductive isolation. But this is to concede that instances of *Canis familiaris* can differ from each other with respect to *any* putative essential, intrinsic property, and so to imply, in effect, that all such properties are non-essential for being such an instance.

This familiar point – that traditional essentialism is false of species taxa – has been taken by some to suggest that species are not natural kinds at all but individuals. As I have argued elsewhere (Wilson 1999, 2005: ch. 5), I think this further claim, and the inference to it, are mistaken. The point I want to underscore here, however, is something that I share with proponents of this individuality thesis: that the failure of traditional essentialism reflects the intrinsic heterogeneity of individuals within a given species taxa. Yet that failure is more general, for the kind of intrinsic heterogeneity that exists in this case can be found across the biological sciences. This has broader epistemic implications that relate to Burian's contextualism about bioknowledge.

Burian doesn't engage in a discussion of the issue that I have outlined above, but there are several places that suggest this kind of metaphysical picture as lying in the background of his discussion. In his essay on model organisms (''How the Choice of Experimental Organism Matters''), he states that ''the evaluation of theoretical knowledge in biology is deeply dependent on a broad base of knowledge about the particularities of different organisms and their alternative biochemical mechanisms, life cycles, means of survival, strategies of reproduction, and so on.'' (p. 14). The conclusion he draws is that the epistemic evaluation of ''theoretical hypotheses in biology is thoroughly comparative'' (p. 14). True enough, and I assume that the implicit contrast with, say, ''theoretical hypotheses in physics'', is to be taken for granted. But one wants to ask *why* this is true, why the ''particularities of different organisms'' matters for a proper understanding of the epistemology of biological practice. One concrete and direct way in which the intrinsic heterogeneity of the living world manifests itself in biological practice is in the need to recognize both the crucial constructive work that model organisms play in developing biological knowledge and the limitations of such model systems as they confront the diversity of the world. To return to an example we have already introduced, we understand the process of eye formation because we know something of its operation in a range of model organisms. But that concentration also allows us to uncover further complexities and differences between the particular realizations of this process in different locational, organismal, and environmental contexts.

Contextualism and Bioknowledge II: Complexity, Pluralism, and Metaphysics

This brings me to a second theme just beneath the surface of Burian's contextualist epistemology of bioknowledge: the complexity that exists both within and between the various levels of biological reality. Consider genes. A common theme emerging as a kind of antireductionist consensus on the concept of the gene over the past 20 years has been that far from providing the empirical basis for the reduction of a "Mendelian" to a "molecular" conception of the gene, molecular biology has justified the rejection of that reduction. An exaggerated way to express the situation would be to say that every time someone articulates a conception of the gene that does useful work in biology in some context (e.g., a gene is a segment of DNA that codes for a protein), there is an empirical finding, often molecularly based, that constitutes a counter-example (e.g., the identification of regulatory sequences) to it as a general concept of the gene.

Biological processes are complex, and are often themselves hierarchically structured. There are molecular genetic effects, but as developmental systems theorists, such as Oyama (2000) and Paul Griffiths (Griffiths and Gray 1994) have emphasized, those effects typically require much additional machinery beyond the genes themselves (see also Jablonka and Lamb 2005). Chromatin marking systems in a wide range of organisms, *Buchera* bacteria in aphids, and even environmental structures, such as nests or hives in burrowing organisms, are three by now standard examples used by developmental systems theorists to challenge claims to the effect that genes play an asymmetrically privileged role in one or another biological process. One of the primary responses to this kind of challenge to genocentric accounts of development, inheritance and evolution has been to argue that such complexity to ontogenetic development and heredity can be accounted for within the gene-centered framework by viewing everything other than genes as providing the *context* for the agency of genes. On this view, chromatin marking (e.g., through DNA methylation), infection by *Buchnera*, and interaction with an existing nest are best viewed not as processes that involve "developmental resources" on a par with genes, but as processes in which specific suites of genes are activated and perform their roles as the agents of development, inheritance, and evolution *only in specific kinds of contexts and given certain background conditions.*

These two views at least appear to present two very different metaphysical views of genes and their place in biology, although aficionados of the Gestalt-switching metaphor that Richard Dawkins (1989) appropriated in describing the relationship between individual selection and genic selection in the second edition to *The Selfish Gene* might well argue that this difference is merely apparent. Again, Burian himself remains relatively silent about where he stands on the metaphysical gap between these two kinds of view of development and evolution, and on this kind of neckerphilic pluralism. But it would be in keeping with the kind of appeal he makes to context, and with the overarching pluralism that he embraces across these essays, to view him as likely to be more sympathetic to developmental systems theory than to context-sensitive individualistic views of development and evolution. What Burian says at the end of his essay "Adaptation" about the gene as unit of selection seems to capture much about his general attitude about such issues:

> the general moral ... is not that the gene is *not* a unit of selection. (It is.) Rather, the moral is that there are units of selection at many hierarchical levels and that we must take into account interactions that cross these levels. The result will be a considerable, but inevitable, increase in the complexity of evolutionary theory, for it means that we will have to examine the strength of the interactions between selective processes at various levels (pp.78–79).

We might want to push further on whether there is a metaphysical view that underlies Burian's epistemology here, or whether it is, if you like, naturalistic epistemic deference all the way down.

Conclusion

In the last two sections I have been suggesting that Burian might well be accused of being metaphysically coy in these essays. But I mean to leave open the possibility that, for someone with Burian's own strongly naturalistic methodology, this call for him to come clean on the metaphysics that accompanies his contextualist epistemology, simply misses the point: it is a kind of remnant of the kind of generalist, one-size-fits-all view of science associated with the positivism that he has left far behind. My own view, for what it is worth, is that one can engage in a lot more substantive metaphysics than Burian does without straying too far from the naturalistic ballpark that he rightly insists on playing in. Whatever one thinks here, Burian's integrative, localistic approach to bioknowledge has provided us by example with a sense of the futility of settling for simple answers to complicated questions.

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