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COMMEMORATION

Remembering Richard Lewontin (1929–2021)

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Richard C. Lewontin, who died earlier this year at age 92, is widely considered to have been the preeminent population geneticist of the last half century (Fig. 1). His work, however, often cast a skeptical eye on his own field, pointing to its limitations as an explanatory framework, as well as the social misuses to which it and allied gene-centric paradigms were prone. By bringing developmental and ecological considerations to bear on narratives of organismal change he helped open the way to a more expansive theory of evolution.

Among the many unusual facets of Lewontin's legacy was the part-conversion of his Harvard laboratory into a latter-day School of Athens, where philosophers, historians, and other scholars in the biological sciences would visit for months at a time, not (per contemporary academic culture) to work on grant-oriented projects, but to observe a master at work and exchange ideas. In this special memorial section of *Biological Theory,* we present the reminiscences of a group of such visitors, of his first "philosophy postdoc" (from his earlier time at the University of Chicago), and of an inheritor of the scientific field that Lewontin did so much to transform. All have become major voices in their disciplines and record the imprints their host and mentor made on their intellectual lives.

Stuart A. Newman

Remembering Dick Lewontin

I spent the 1990–91 academic year visiting Dick Lewontin's lab. Intellectually, this has been the most exciting year of my life (so far). Lewontin was – and is – popular and influential among philosophers because he understood what we are up to and respected what he referred to as the "craft" of philosophy. I see this side of him as a consequence of something more basic, though. This is the unusually integrated nature of his intellectual outlook and pursuits. Everything he did fitted together.

During the first semester, three times a week I'd walk from Somerville to the Museum of Comparative Zoology,

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Fig. 1 Richard Lewontin, Mary Jane Lewontin, Jura Newman; Devil's Dyke, Sussex, UK, fall 1971; photo: Stuart Newman

arriving at 8:30 am, for Lewontin's introductory lectures on statistics in biology. Lewontin would stand there in an old lecture hall with no notes or books, just a big blackboard and two colors of chalk – I think blue and white, but I am not sure. One color was used for the real world (parameters characterizing the population of interest), usually higher on the board, and the other color was for the world of observed samples. He had an entire semester-long statistics course, one laced with philosophy and a good deal of history, sitting there in his head. Many students were there just to learn how to do a *t* test or ANOVA, not to think about the underlying principles, but I think even the most practically minded students tended to imbibe, and benefit from, the big picture and the larger questions in play. Here we are in the world of the sample, making inferences about what lies behind it, based on an imperfect model of how those observed cases made their way to us. A characteristic Lewontinian combination of themes – the world is complex and knowledge is difficult, but we should push ahead and try to get something done – was persistently explored in those introductory lectures.

This continual presence of big-picture questions, in combination with focused empirical work, made Lewontin comprehensible and exciting to philosophers. Unlike some scientists, Lewontin did not combine an interest in philosophical questions with a degree of disdain for the discipline itself (Hawking, Dawkins). Lewontin liked the philosophical tradition and some parts of the practice of philosophy, though I think it was the "how things, in the broadest sense, fit together" (compressing Wilfrid Sellars) orientation of philosophers that was more fundamental and made these relationships work well. Within philosophy, there was particular engagement with epistemology, together with what can be called "philosophy of nature," a scientifically informed exploration of basic characteristics of the world of a kind that overlaps with metaphysics. Lewontin was ambitious in science, but mindful of limitations in our epistemic situation and the problems posed by complexity and historicity.

Another side of this intellectual integration, and a link to another part of philosophy, is seen in Lewontin's political engagement. In Jerry Coyne's reminiscence of Lewontin on his website, he makes a point of emphasizing a basic separation between science and politics: "Dick was an avowed Marxist, and on this we disagreed. But he kept his lab's science separate from his politics, and it caused no friction."[1] In Coyne's sense, this separation certainly did exist, as far as I can tell. I don't say that absolutely any political orientation would have been welcome, but there was no imposition or pressing of anything like Marxism. However, a political dimension was usually intellectually present – a turning-over of political questions, an eye to the political economy of science. By the time I was in his lab, about five years after he and Levins published *The Dialectical Biologist* (Levins and Lewontin 1985), I had a sense that Lewontin's own Marxist commitment had a degree of lightness. In our discussions he referred to a Marxist "influence," rather than a Marxist position or conviction. My sense was that his partial skepticism,

[1] https://whyevolutionistrue.com/2021/07/05/dick-lewontin-1929-2021/.

or (to use more recent philosophical terminology) epistemic humility, occupied a more central position than anything like a doctrinal Marxism.

The intellectual integration I have emphasized in this note was probably the strongest positive influence, among many, that I took from the year in his lab. One can live pretty far from *Drosophila* genetics, two-locus theory, statistical methods, and Marxism while taking Lewontin as a model in this respect. I thought at the time that his lab was an ideal, almost a Platonic one, of an intellectual community, and that is how it still seems in memory.

Peter Godfrey-Smith

Dick Lewontin, My Godfather

By the term "godfather" in the title I do not mean the Mafiosi definition, but rather that of the Roman Catholic Church. In that rite, a godfather sponsors an infant in baptism, pledging to lead his charge in intellectual growth and to serve as an adult role model. Dick Lewontin served this role for me. His role was not to enrich my spirit, but I did learn some church history from him. In condemning Arthur Jensen’s treatise about race and IQ, Lewontin (1970a) cleverly compared him with Dutch Bishop Cornelius Jansen (1585–1638). Jansen taught that certain people were predestined to be saved, others damned, good works irrelevant, and free will an illusion. Jansenism was condemned as heresy by Pope Innocent X in 1653. In analyzing the twentieth century Jensenism of race and IQ, Lewontin (1970a) argued that Jensen's treatise revealed unconscious bias about racial inequalities that constituted "a doctrine as erroneous in the twentieth century as in the seventeenth." Tongue in cheek, he wrote, "I shall try to play the Innocent." Combating racism was one of Lewontin's lifelong ambitions.

Dick would likely be horrified for me to extoll him as a role model in the religious sense, but in the secular sense that I intend, I hope he would be mollified. In guiding my professional life, and serving as scientific role model for someone just starting out, he was my godfather. Why he singled me out for his good works is, to this day, beyond me. His efforts on my behalf were acts of selfless generosity for which I am forever grateful.

My first encounter with him was in 1967 when I was a graduate student in James F. Crow's group at the University of Wisconsin, Madison, and we made one of our occasional road trips to Chicago to exchange presentations and ideas with Lewontin's group. I presented evidence that *segregation distortion* in *Drosophila melanogaster* was associated with sperm dysfunction rather than the prevailing view that it had something to do with how bivalents align on the metaphase plate during meiosis (Hartl et al. 1967). Dick suggested a follow-up experiment. I thought about it for a few moments and said that his experiment would seem to require a prodigious amount of work. He put me in my place by mumbling something about research never being easy.

Me being put in my place, we got along well, and overall there was great mutual respect and admiration between the Crow and Lewontin groups. Dick sent Crow a flimsy carbon copy of an early draft of the now-famous Lewontin and Hubby (1966) paper, and I well remember the lively discussions we had about what the apparent abundance of protein polymorphisms implied about population genetics and evolution.

It's hard to exaggerate the influence of the Lewontin-Hubby paper. It turned population genetics on its head. What had been a data-poor field with a rich theory that asked what might happen under imagined conditions became, virtually overnight, a data-rich field needing a new theory that asked what evolutionary or demographic processes could account for an actual set of observations.

A summary of the vast effort that went into protein electrophoresis can be found in Nevo (1978). That era ended with the ability to study DNA polymorphisms (Kreitman 1983; Sawyer et al. 1987), but by then it had already become clear that the interpretation of protein polymorphisms was compromised by an unknown mutational spectrum among electrophoretic alleles and the inability to distinguish identity by descent from identity by state.

In retrospect, what were the upshots of that era? One was that the focus on protein polymorphisms sucked the air out of much other research in the field, as many population geneticists turned their attention to running gels. Those who went their own way were often regarded as sidelined or out of step. Looking back some 25 years later, Lewontin (1991) admitted the missed opportunities with regret.

A second upshot was a long, vociferous, and sometimes acrimonious split in the field between the "neutralists," championed especially by Kimura (1968), and the "selectionists," argued forcefully by Wills (1973). The dispute was ultimately futile because it assumed implicitly that genes evolve independently of one another when in reality they evolve along with their near neighbors in the chromosome. While many nucleotide mutations are now regarded as having little or no effect on fitness of their own, their ultimate fate may nevertheless be determined by what happens demographically or evolutionarily to the chunk of chromosome in which they happen to reside (Hartl 2020).

On the plus side of the ledger was a burst of new theory. Much of it is now obsolete as it addressed various issues specific to protein variants detected by means of electrophoresis. But one direction was exceptionally fruitful and invigorating. This was Warren Ewens's sampling theory of neutral alleles (Ewens 1972). This was the first theory that asked what evolutionary processes could be inferred from an observed set of molecular data. Ewens challenged his friend, the outstanding British mathematician Sir John Kingman, to find a generalization, to which Kingman replied that he enjoyed working on such problems as light entertainment when on aeroplanes. A few years later he informed Ewens that he had found an approach that would apply to his sampling theory as well as to many other problems. What was the approach? The coalescent (Kingman 1977, 1982). This fundamental concept stimulated much theoretical research and data analysis for the next two decades.

After my Ph.D. at Madison and a brief postdoctoral stint at Berkeley, my next encounter with Lewontin took place when he responded favorably to my invitation to visit the University of Minnesota. It was quite a coup for a starting assistant professor to get someone of his stature to come for a seminar, and Dick was very generous to agree. He took the train from Chicago because he disliked flying, and on the way he analyzed a theoretical model in which he showed that restriction of recombination increases fitness (Lewontin 1971). This was, I think, a forerunner of Feldman's principle that, in many but not all situations, modifiers that reduce recombination are favored (Feldman and Liberman 1986).

It was in this period of his professional career that Lewontin was among the first to exploit an ever-expanding computer power, which included numerical solutions to multiple equations (Lewontin and Kojima 1960) and iteration of complex models (Lewontin 1964).

For some years after our meeting in Minnesota, Dick tilted at his windmills and me at mine, and we seemingly went our separate ways. But then, one day early in 1991, he called me to suggest that we should write a paper together on shortcomings of DNA typing as it was then being practiced. The story is told in detail in the *New York Times* of December 20, 1991 (Kolata 1991). In brief, the story is that Lewontin and I had written and submitted an article to *Science* disputing the notion that DNA fingerprinting could identify a suspect with only a negligible chance of error. Shortly thereafter I got a call from a federal prosecutor in the U.S. Department of Justice, who told me that he felt that publication of the paper would be a disservice to the system of justice in the United States. I told Lewontin about this call, and he sent off a scathing letter to the prosecutor saying, "When someone who is an official in the Department of Justice Criminal Division Strike Force telephones a private citizen to request an action the citizen would not ordinarily take, then a form of intimidation has been used."

The prosecutor then called me, wanting to know whether I had recorded his previous call. (I had not, as a matter of principle.) He then asked if I had felt intimidated by his earlier call. I told him that his call had stunned and chilled me, and that he certainly did make me feel intimidated.

While all this was unfolding, the *Science* paper had been reviewed and accepted. But then the editor interjected himself. He said he wanted us to soften our conclusions or withdraw the paper and resubmit it as a short opinion piece. Lewontin flatly refused. He later told his interviewer: "We finally did make some changes, against my better judgment" (Kolata 1991).

At this point in the publication process the editor-in-chief of *Science* took upon himself the unprecedented step of commissioning an article to make a point-by-point rebuttal. He then delayed publication of our paper until the rebuttal could be published in the same issue (Chakraborty and Kidd 1991).

Looking back on these events many years later, my impression was that Dick seemed invigorated by the experience, while I found it extremely stressful. This was my fifteen minutes of fame, and that fifteen minutes was more than enough fame for me.

A few years later, in 1993, supported by a search committee consisting of Wally Gilbert, Matt Meselson, and Dick Lewontin, I was recruited to Harvard and finally came to know Dick Lewontin as a wise and treasured colleague as well as a friend and godfather. But that's another and much longer story.

Daniel L. Hartl

Il Maestro Di Color Che Sanno

Pierre Duhem, the eminent French historian and philosopher of science, divides scientific minds into two types. The English mind, exemplified by Napoleon, is broad but shallow. The French mind, one like Newton's, is narrow but deep. Duhem seems to overlook a possibility: that the intellectual virtues might be combined. But then, he had never met Dick.

I was more fortunate than Duhem. In the fall of 1981, I spent my first sabbatical at Harvard's Museum of Comparative Zoology. I had come for a year, to repair some of the inadequacies of my knowledge of biology, and Steve Gould had given me space. In an early conversation, Steve suggested that attending Dick's weekly lab meeting would be a good idea. But that advice was unnecessary. The philosophers' bush telegraph had already made that public knowledge.

What struck me immediately was the constant intellectual vitality, the combination of seriousness and playfulness – and the irreverence. At an early meeting, Dick announced that he would be absent for one of the upcoming sessions. He would be attending a conference. The topic? Recurrent problems in evolutionary theory. To which one of the attendees responded, with a wit worthy of Dick himself: are you a speaker, or the topic?

Apt enough. Dick was a great unsettler of people's established opinions. In his lab meetings and in his lectures, he would bring his hearers up short, provoke them to a defense, and show how it collapsed. And even more vibrantly in conversations. Exchanging ideas with Dick has been one of the effervescent pleasures of my life, during the year in Cambridge and ever since. Sometimes we have agreed, and even stood shoulder to shoulder – in critiques of human sociobiology and its spinoff, Santa-Barbara-style evolutionary psychology, as well as in emphasizing the social embedding of science and the social responsibilities of scientists. On other topics we've been at odds, holding opposing views on the units of selection and different perspectives about how to understand genetic determinism. It is hard to say which have been more enjoyable, our alliances or our arguments.

There's a reason for that. "Science" acquired its modern meaning only in the nineteenth century. Before that, the accepted term for theorizing about nature was "Natural Philosophy." (Indeed, well into the twentieth century the other Cambridge's course in the sciences was known as "The Natural Philosophy Tripos.") Dick was a natural philosopher in both senses of the term.

So it's no shock that contemporary philosophy of biology has been developed at his knee. Year after year, philosophers of science interested in biology came to Harvard for their apprenticeship with Dick. My own collection of essays in philosophy of biology records a debt I am hardly alone in feeling. Its dedication – to Dick and to the memory of Steve – pluralizes a famous line from Dante's *Inferno*, where Aristotle is characterized as "the teacher of those who know" (*il maestro di color che sanno*). A wonderful letter from Dick let me know how tickled he was by my borrowing. A lover of poetry, Dick counted Dante as a special favorite – and was prepared to argue about him with Italians, in Italian.

To count myself as one of "those who know" isn't self-flattery. Like others, I know because Dick taught me so much. And, in advance, we knew enough to seek him out, because he was, so evidently, the master.

Nor was his teaching confined to biology. By that I don't simply mean that he could teach anyone a great deal about music and poetry and politics and history and … He also taught those who knew him about life. To spend an evening with Dick and Mary Jane was to recognize the reality of deep and abiding love.

I saw him for the last time when the three of us had lunch at Cadbury Commons. As I knew in advance, Dick's short-term memory had almost entirely disappeared, and the conversation proceeded in five-minute bursts. Until I inadvertently tapped a rich vein of intact memories about a topic we'd discussed decades ago. Suddenly, the old Dick was in full cry, picking up the threads as if we'd started our conversation only the day before. Mary Jane could scarcely see and barely hear. Yet she sensed what had occurred. And her face was aglow.

Enjoying Dick's friendship was an enormous privilege. I shall not look upon his like again.

Philip Kitcher

Richard Lewontin and Auto/Biography

Between 1996 and 1998, we conducted a series of lengthy interviews with Richard Lewontin (hereafter "Dick"), a compressed version of which was intended for publication in a Festschrift volume (Lewontin et al. 2001). It was an excruciating experience for everyone, with the conversation nearly ending before it began. We had provided our subject with a tentative list of questions. An excerpt from the first paragraph of the interview gives a sense of both the tone and content of his reaction:

> I was somewhat alarmed when I read the list of questions, beginning as they do with personal issues, parents, upbringing, political life, college, and so on. The question is … what the posing of them reveals about what we are engaged in here. I assumed that we were engaged in a piece of oral history in which an interview with a participant in population genetics during an era when it was being founded, in a sense, … and when it underwent major changes would be interesting because there would be firsthand recollections of events, people, and ideas that were not available through the written record. … I take it that is the purpose of oral history, but none of that has anything to do with the personal history of the actor. (Lewontin et al. 2001, p. 22)

Despite concerns about his interviewers' aims, he finished the interview (and four others).

In retrospect, his reaction should not have surprised us since he had earlier objected to biographical approaches to the explanation of historical and sociological phenomena. Indeed, he disliked biographies and autobiographies, said he never read them, and was perplexed by their appeal to others. His distaste for biography/autobiography may in part reflect the fact that he was an intensely private person, who did not easily share intimate details of his personal, familial, and inner life or expect such details to be shared with him. It may have seemed intrusive to inquire of others about personal matters, but he was also not very curious about them. (This may explain why he was also baffled by the craze for learning one's "roots" and the popularity of genealogical research and testing.) Although biography is often viewed as a tool to capture and hold the interest of readers and engage their emotions, the kind of details that many others would find fascinating, he instead found dull. As we will see, he also considered such biographical "facts" to be both extraneous and untrustworthy.

His intellectual reasons for disliking biography were perhaps most clearly articulated in a sharply critical review of Daniel Kevles's *In the Name of Eugenics* (Olby and Lewontin 1986). Although he found much to praise in the book and shared the author's ideological sympathies, he disparaged Kevles's biographical approach to the subject. Perhaps predictably for a Marxist, he complained that such an approach attributed too much importance to individuals and not enough to the social factors that explain why particular ideas gain currency at a particular time. This was an oft-repeated theme in his writing and lectures. Applied to the history of science, it implied that individuals had only minor impacts on the trajectory of scientific programs. Thus, later in our interview he circled back to his remarks at the start, invoking his mentor as a test case for the significance of individuals in creating and shaping scientific fields: Theodosius Dobzhansky "was a person of such immense strength of personality and drive" that, "If it can't be shown that Dobzhansky had such an effect, then it would be impossible to show it for anybody else." But even here, the "hypothesis of personal influence fails" (Lewontin et al. 2001, p. 23).

Thus, one objection to a biographical approach was that it overstated the historical significance of individual belief and action. Another was less conventional. In Dick's view, at the individual level, scientific beliefs were underdetermined by political allegiances, by personal factors such as family relations, religious upbringing, education, or social status, and by broader economic, social, or political circumstances. In regard to the first, he denied (not always consistently) that there was any straightforward alignment between sociopolitical and scientific beliefs, for example, noting that, in the history of eugenics, the positions "of the Marxist J. B. S. Haldane, of the liberal Julian Huxley, of the conservative Ronald A. Fisher, and of the racist and reactionary Edward M. East have many elements in common, especially in their views about the relevance of genes to human temperamental and intellectual differences and to the unequal distribution of these genes in different races or social classes" (Olby and Lewontin 1986).

Similarly, in an otherwise favorable review of Steve Gould's *Wonderful Life* (Lewontin 1990), Dick criticized his colleague's biographical approach to the positions of his actors on the grounds that the broader political commitments and social backgrounds of the protagonists do not explain their differing interpretations of the Burgess Shale fossils. In his view, Steve had applied an ideological analysis of science at the wrong scale:

> Certainly people see nature through a glass molded by social experience. Darwin's theory of evolution by natural selection is obviously nineteenth-century capitalism writ large, and his immersion in the social relations of a rising bourgeoisie had an overwhelming effect on the content of his theory. … Class matters, but it is not determining for individuals. As the inventor of the modern theory of class reminded us in the third thesis on Feuerbach: "The doctrine that men are the products of circumstances and upbringing … forgets that it is men that change circumstances."

Thus, the biographical method can explain neither the social uptake of ideas that originate in an individual mind nor why an individual came to their beliefs. He scoffed at Michael Ruse's linkage of his critique of sociobiology to his Jewish upbringing (Ruse 1999), not only because he was raised in a completely assimilated family but because facts about personal history, even if they were reliable, have only modest explanatory power.

But in his view, they are *not* reliable since the data on which biography depends is inevitably anecdotal. Dick would have agreed with Sigmund Freud when Freud wrote in a 1936 letter to his friend Arnold Zweig, who had expressed interest in becoming his biographer: "Anyone turning biographer commits himself to lies, to concealment, to hypocrisy, to flattery, and even to hiding his own lack of understanding, for biographical truth is not to be had, and even if it were it couldn't be used" (Armstrong 2015). In Dick's view, biography "has few independent intersecting streams of evidence. It depends almost entirely on the actors' self-reports and on the reports of other members of the scientific community, who participate in a community of gossip and conventional wisdom that circulates about influential or contentious figures, filtered through the biographer's own life history" (Olby and Lewontin 1986).

This objection is congruent with his broader epistemological stance. As the editors of the Festschrift volume noted, Dick was "well-known — even infamous — for persistently questioning whether geneticists and evolutionary biologists can possibly know what they want to know and often claim to know" (Singh et al. 2001). Some scientific colleagues found his standards demoralizingly high. Ward Watt once complained at a meeting convened to discuss the state of population genetics, where Dick had asserted that the field had failed to provide "authoritative explanations" of what really happens in nature and was far less rigorous than its use of statistics made it appear: "You can't make any progress in science by discouraging people" (Wheeler 1997). Dick was unfazed by the rebuke. Throughout his career, as Michael Ruse (1999) has observed, he remained determined "to play by the strictest of epistemic rules" (see also Segerstråle 2000; Beatty 2009). Thus, Dick was skeptical of biography and autobiography in large part for the same reason that he was skeptical of so much work in population genetics, evolutionary biology, and agricultural and behavior genetics: he thought that claims in these fields went beyond what was proved – or was even possible to prove – and that the failure to achieve what he called "empirical sufficiency" characterized not only particular domains of science but also the writing of history.

However, we would be remiss in not acknowledging that Dick was sometimes inconsistent in his attitudes toward biography, at times implying that individuals' ideas could in fact be attributed to political or other ideological allegiances or to social circumstances. In the interviews, we noted that in his classic *The Genetic Basis of Evolutionary Change* (1974, p. 29), he had invoked the divergent ideologies of Dobzhansky and H. J. Muller to explain (in part) the source of the "classical-balance" controversy that had so importantly shaped the field of evolutionary genetics. We asked why ideology played a role in his textbook presentation of the field whereas in the interview he had recounted developments in evolutionary genetics "as an almost pure logic of ideas." To this challenge, he responded somewhat unsatisfyingly, that, well: "Biographical information [in this case concerning Dobzhansky's politics] *can* be revealing."

That Dick struggled with how personal factors and social circumstances influence an individual's scientific beliefs, how an individual's political and scientific beliefs may align, the place of an individual in history, and his own place in the history of science, is evident in remarks at the end of our first interview:

> What I guess I'm saying is I find a certain consistency between general world view, political ideology, and attitudes about scientific questions. I'm not saying they're determinate. I'm not saying there aren't variants. My problem, as a person trying to talk about the history of ideas, is that I'm confused. I don't have a doctrinaire position on the relative importance of individuals and their predilections, and how that comes together as social movement. That's a problem we haven't solved, any of us, and I haven't solved it in my own mind. To say that no individual matters is clearly wrong, but to write the history of science as a history of individual careers is also clearly wrong. (Lewontin et al. 2001, p. 43)

We think that passage reflects not just his intellectual struggles but his intellectual honesty. Dick certainly had a polemical, take-no-prisoners, side, but also and much less noticed, a rare willingness to openly acknowledge not just confusions, but changes of opinion, contradictions between theory and practice, and compromises made to advance his career (even when such admissions required sharing personal anecdotes).

In the interviews, he explained that population genetics originally appealed to him because he (mistakenly) considered it wholly irrelevant to political and social issues. He had been politically active in high school and initially in college. But he found himself expelled from Harvard with no career prospects and a wife and child to support. Given an opportunity to be readmitted, he thought, "*oh-oh, I've got to make up for this catastrophe in my life – I've got a family to support* [italics in original]. So I turned my back on any political or other extracurricular interest; I deliberately turned my back on all that and just became very careerist," even crossing a picket line when he was a graduate student at Columbia (Lewontin et al. 2001, p. 27). We venture to suggest that most people would be inclined to bury such an ignominious episode, but as this passage demonstrates, Dick could be as ruthlessly critical of his own as he was of colleagues' scientific and extra-scientific practice. Regarding his own behavior, it can be said that he did his best to adhere to Marx's dictum in the *1844 Manuscripts* that "one basis for life and another for science is a priori a lie."

Diane B. Paul and John Beatty

In Memory of Dick Lewontin

Richard Lewontin's passing on the 4th of July marks the end of an era for radical science in the United States. In death, his long-time collaborator, Richard Levins, had preceded him in 2016 and Stephen Jay Gould, the third member of Harvard's most distinguished triumvirate, had died in his relative youth, almost twenty years earlier in 2002.

For a biologist and philosopher coming of scientific age in the late 1970s and early 1980s, Dick Lewontin was a towering figure not just because of his science but because of his public commitment to social justice. At Columbia University, where I was an undergraduate, we were glad to have him as an alumnus. Many of us had already worked our way through his dissection of heritability analysis and its irrelevance. Lewontin (e.g., 1970a, b) was a bastion against the scientific racism of figures such as Arthur Jensen, William Shockley, and, in a more subtle form, found in the human sociobiology of E. O. Wilson. He laid the foundation for our understanding of human genetic (and genomic) diversity within and between groups that are resplendent in their cultural diversity in spite of biological homogeneity. That foundation is periodically under attack by new avatars of a desperate scientific racism, but, now as in Lewontin's time, these attacks reflect the structural disparities of social power rather than any credible biology.

I first met Lewontin in 1982, through the intermediation of Bill Wimsatt (also one of the participants in this commemoration), when Lewontin spoke at the University of Chicago at an event to mark the centenary of Darwin's death. Tellingly, while this was a lavish occasion at that university, nothing marked the perhaps more important anniversary a year later, of when Marx followed Darwin to the grave. In later years, Dick and I mused over that.

In the early 1990s I spent two years partly in Lewontin's lab at Harvard while being on the faculty at Boston University and a fellow at the Dibner Institute at MIT. Diane Paul (another of our participants here) and I shared an office, and I inherited the space from Raphael Falk, who also died recently (Sarkar 2021). Lewontin came in about once a week, on the Wednesdays that the lab had a seminar, and those were the occasions on which I mainly interacted with him. The seminars had a university-wide reputation and, on one occasion when I was speaking on heritability (in 1995), even Ernst Mayr showed up. Mayr did not say a word, which was rare for him. Later he was surprised that Lewontin had not disagreed with my deviation from some work he had done with Marc Feldman (Feldman and Lewontin 1975).

Lewontin introduced me to Jon Beckwith, who was one of the organizers of a genetic discrimination study group that had been spawned by the Science for the People movement of the 1970s. Discussions in that group helped develop the critiques of the Human Genome Project that Fred Tauber and I published early in the 1990s (Sarkar and Tauber 1991; Tauber and Sarkar 1992, 1993).

My most vivid intellectual memories of Lewontin come from a graduate seminar in the philosophy of biology organized in spring 1991 by Amartya Sen and Robert Nozick. The participants included Gould, Falk, and Lewontin. Faculty sat in an inner circle with the organizers; students were relegated to an outer circle. Faculty talked interminably and disagreements were severe. Sen took joy in pointing out how often Nozick inadvertently invoked Marx. I have no recollection of a student ever saying a word. Lewontin dominated that seminar, and Falk and I often met later over coffee to mull over his remarks.

Arguing with Lewontin about the units of selection in that seminar led to my perspective that genes versus organisms was a false dichotomy. In his famous 1970 paper on the units of selection, Lewontin (1970c) had pointed out the potential conflicts between levels of selection. But, within the organism, he had not mentioned genes; rather he had mentioned gametes. From my perspective, genes and gametes belonged to different hierarchies of life (Sarkar 1998). I am not sure that I ever convinced him of a view I associate with George Williams: that the organism could be the unit of selection and that selection could favor one gene (allele) at the same time. But he listened, and that is the part of him that made him such a dominant influence on the philosophy of biology.

As we move forward, we will miss Lewontin's towering intellect in biology. But, even more than that, we will miss his understanding of science as an ideological construct reflecting social relations, as much part of the superstructure as forming the base, to use terminology from a shared Marxist framework. Keeping that understanding alive, reminding ourselves that science is valuable primarily as a possible tool of liberation, would be the best way to honor Lewontin.

Sahotra Sarkar

Richard Lewontin—a Life Changer

As a fledgling assistant professor at University of Wisconsin–Madison, with no training in biology or its philosophy, I read Bill Wimsatt's (1970) review of George C. Williams's (1966) *Adaptation and Natural Selection.* Bill's comments about evolutionary epistemology made me curious, so I read Williams's book; I thought it was a philosophical gold mine. This led me to read Dick Lewontin's (1970c) article "The Units of Selection." I was captivated by Dick's characterization of evolution by natural selection as a kind of process that can occur at multiple levels of organization. This resonated with a kind of anti-reductionism that was and is very popular in philosophy of science. I also was struck by Dick's empirical approach to the problem (as witnessed by his discussion of the t-allele in mice and the evolution of reduced virulence in myxoma), which contrasted sharply with Williams's often a priori arguments, and also with the contemptuous view of group selection that Richard Dawkins propounded in his (1976) book, *The Selfish Gene*. I wrote a letter to Dick, introducing myself and asking various naive questions. Dick replied with detailed comments, and so our correspondence began. I then organized a small conference on group selection here at Madison in 1979, with Dick, Mike Wade, David Hull, and Bill Wimsatt as presenters. Jim Crow and Sewall Wright were in the audience. I mainly listened.

My first sabbatical was in 1980–81 and Dick welcomed me to his lab at Harvard. The experience there changed my life. I was then strongly committed to Quine's idea that philosophical questions and scientific questions are on a continuum; there is no bright line separating them. I usually talked with Dick twice a week during that year and attended the classes he taught. I felt that Quine's idea was coming to life before my eyes. Dick was passionate about the need to analyze central concepts in evolutionary biology. His (1978) *Scientific American* article on adaptation struck me as a beautiful example.

Dick's influence on me extended beyond these academic matters. My wife, Norma, and I saw Dick and his wife, Mary Jane, socially during that year. They were 20 years older, but they felt free to talk about personal matters with us, and this made us comfortable to do the same with them. We discovered our shared love of chamber music. That winter, we visited Dick and Mary Jane in Marlboro, Vermont, where they had a log house that he and Richard Levins had built from a kit. After the sabbatical, we returned to Marlboro a few times and went to concerts with Dick and Mary Jane at the summer music festival there. I fondly remember Norma and Dick singing in the festival's season-end performance of Beethoven's "Choral Fantasy."

During the year in Dick's lab, I met John Beatty and read his review with Bill Fink of my (1975) dissertation-turned-book on parsimony (Beatty and Fink 1979); their review was where I first learned about cladistics, which rekindled my interest in Ockham's razor; I have worked on parsimony on and off ever since. I also met Steven Orzack in Dick's lab; he and I have had several fruitful collaborations. 1980–81 was an amazing year for me.

Dick has sometimes been described as a foe of natural selection, a dogmatic Marxist, and a tragic figure. The truth about the first of these is that he was a foe of what he took to be *naive and uncritical* invocations of natural selection. As for the Marxism, Dick and Stephen Jay Gould did connect their opposition to sociobiology to their Marxism, but I think their criticisms of sociobiology were independent of Marxism. Their politics *motivated* them to go public with their criticisms, but the *content* of those criticisms was scientific. The alleged "tragedy" is that Dick's work with Jack Hubby on electrophoresis in the 1960s was Dick's stand-out contribution to science, and yet that work was reductionistic, thus contradicting Dick's avowed anti-reductionism. I think that Dick's scientific contributions go well beyond the work he did with Hubby. In addition, classifying that work as "reductionistic" is a mistake. True, it was about measuring genetic variation in populations, but that doesn't make it reductionistic. Dick thought that the evolution of genes is an important topic, but that doesn't mean that it is the only or the best way to think about evolution. It is well to remember that Dick's 1970 paper on units of selection denies that group and individual selection reduce to genic selection (Lewontin 1970c).

The distinction between scientific content and political motivation is also relevant to understanding Dick's influential paper "The Apportionment of Human Diversity" (1972), which was about variation within and among races. Dick's politics prompted him to write and publish the paper, but his argument stands on its own. Anthony Edwards published a criticism of Dick's paper in 2003 called "Lewontin's Fallacy" (Edwards 2003). I think that Lewontin and Edwards addressed different questions, and that the fallacy that Edwards describes does not arise in Dick's argument. Dick wanted to compare genetic variation within *populations* with genetic variation between *populations*; Edwards wanted to see if data on an *individual* would allow one to infer that individual's membership in one of several populations.

Dick's impact on history and philosophy of biology was substantial. The historians and philosophers of biology whom Dick influenced and worked with include André Ariew, John Beatty, Robert Brandon, Hayley Clatterbuck, Michael Dietrich, Peter Godfrey-Smith, Oren Harman, Philip Kitcher, Elisabeth Lloyd, Diane Paul, Robert Proctor, Will Provine, Sahotra Sarkar, Bill Wimsatt, and Rasmus Grønfeldt Winther. Dick's popular essays in the *New York Review of Boo*ks were often philosophical. Philosophy of biology blossomed in the 1980s and it continued to thrive; Dick was a big reason why.

Elliott Sober

Dick Lewontin as Natural Philosopher

Dick Lewontin gave a Sigma Xi lecture at Cornell in the spring of 1964, during my second installment as an undergraduate.[2] After three years in Cornell's Engineering Physics program with an increasingly erratic record, I had returned from a year working in industry (designing adding machines) to major in philosophy. Though my father was a biologist, I had planned to do philosophy of physics. Reading Aristotle on teleology intervened. Talk of function and purpose was an important problem to philosophers, who (incorrectly) thought they needed justification. I thought teleology in biology (and perhaps elsewhere) had two possible sources—either the cybernetics of control systems (for goal-directive behavior) or as expressions of what a trait was selected for in evolutionary theory. By then I knew a fair amount of cybernetics, and had sat through a fairly mundane course on evolution. After looking at the cybernetics, I bent over to take a closer look at evolution, and fell in. Dick surely gave me a strong push.

This guy was pacing back and forth, lecturing animatedly without notes, talking and gesticulating, writing algebra and genetics on the board, and occasionally showing a slide.[3] (He must have been 35, but looked like someone you could trust to a generation that was soon to hear that you could never trust anyone over 30.) The contrast was striking: philosophers "*read* papers" —afraid someone would jump down their throats if they chose a word wrong. And scientists "gave talks," with lots of data on slides, and an attitude towards "Just the facts, ma'am" that would have made Sgt. Joe Friday proud.

He talked about new stuff in areas I had thought were settled and quiescent: modelling in biology—in population genetics—seemed new, and raising issues and techniques I had never seen in talk of evolution.[4] He talked a lot like a philosopher —even mentioned Kant—but more daring. Philosopher Tom Goudge had just (1962) written a good book—on the theory of evolution, in which he said that there was a lot going on, but that he was not going to talk about anything before it was settled. But Lewontin was a scientist, so didn't have to wait—he could argue about things he was trying to *get* settled. And this was exciting stuff—multilocus selection and group selection. But like a philosopher, he criticized theories *conceptually*, he didn't just present them. And his work gave new handles on phenomena where

[2] This is a revised excerpt from a longer essay (Wimsatt 1999).

[3] That (and the lecture I heard at Pitt two years later) was before blue work shirts became a regular item in his wardrobe. (At his retirement Festschrift, when Dick turned up, he met an audience of 200 all dressed in blue work shirts.)

[4] Fittingly, it was a paper on modelling (Lewontin 1963) prepared for a Festschrift for philosopher-scientist J. H. Woodger.

there hadn't been any before. Dick approached evolutionary theory like a physicist would, with state-space representations and a variety of models, and in very many ways has deeply influenced my views of evolutionary theories. (His later book (Lewontin 1974) is a paradigm of this approach.)

I had thought computers were things used only in advanced physics, but here Lewontin was programming one—indeed, in assembly language! The only adaptive topographies I had seen were illustrative, but he was showing one with real data from his own work on selection in a two-locus system. It became one of the first things I programmed a decade later. That picture (Lewontin and White 1960) was a resource: I drew on and extended his arguments (Lewontin 1970c, 1974; Wimsatt 1980, 1981) against "single-locus thinking." It was richer and seductively more complex than any single-locus case I had seen, and with his work on group selection (Lewontin and Dunn 1960) became cornerstones of my defenses of higher-level units of selection.

At Pitt, I discovered utility theory. "Just fitness on a weaker metric!" I thought, with a sense of superiority. But then (reading Lewontin and Waddington) I found that they were equally weak: you couldn't do interpersonal comparisons of utility, and you couldn't do interpopulational comparisons of fitness. (Biological optimality was getting messier.) I got him invited to Pitt. When Dick showed up to give the lecture, I had read his pioneering application of game theory to evolution (Lewontin 1961), written a long paper on it myself, and wanted to talk. I attached myself to him as a local guide and spent about 18 hours talking with him in the two days he was there.

Two years later Adolph Grunbaum, senior philosopher of physics at Pitt, asked if I wanted an external examiner on my dissertation. (Philosophers of biology were then virtually nonexistent.) He wasn't surprised at my choice. I soon asked Dick whether I might come study with him as a postdoc. I wanted to work on units of selection, on integrating a more complete picture of the phenotype into evolutionary theory (using my work on functional organization), and on game theory and evolution. And I wanted to learn population genetics from the inside.

He graciously let me come—I was his first "philosophy postdoc"—and even more graciously found me money. I was astounded that he would spend money on a philosopher (instead of another postdoc doing theory or gel electrophoresis (Hubby and Lewontin 1966)) and told him so, but I was delighted to be there. A year later, when a promised position in philosophy at Chicago was eliminated, he tried to extend my postdoc for another year. The deans of biological sciences and humanities finally gave half a year each, with strong nudges from Dick. And my foot was in the door. When I got an outside offer Chicago countered with a regular tenure-track offer, and I've been there ever since. Dick was at least twice-over responsible for my being at Chicago.

Dick brought Dick Levins and Leigh Van Valen to Chicago, and all participated regularly in a new philosophy of biology discussion group along with Stuart Kauffman, Stuart Newman, Arnold Ravin, Marty Zwick, Ken Schaffner, Dudley Shapere, David Hull, me, and students in the new Committee on the Conceptual Foundations of Science—along with many visitors to the Lewontin lab (including John Maynard Smith for a quarter)—a remarkable "critical mass" for the new philosophy of biology. The strong participation of scientists has marked the discipline ever since.

A focal point for me as for many others was the two-quarter population biology course (305–306) that he and Levins cotaught, in which both were generally there together. It was sufficiently different each year that many sat through it several times. Only Lewontin could think fast enough to stop Levins in mid-derivation, so we understood Levins better when Lewontin was there; Levins similarly fleshed out some of Lewontin's ideas with examples and models. After class they both usually held forth in the coffee room to most of the postdocs and anyone else who cared to join. The discussions ranged over all of evolutionary biology, and culture and politics as well, and provided a chance to try out all sorts of ideas.

Being in Dick's lab those 18 months was the most exciting intellectual period of my life, and has intersected with most of my projects since. He has probably had a greater influence on the character of philosophy of biology as now practiced than any other scientist. (Dick Levins is perhaps comparable, while Ernst Mayr's impact has declined substantially.) Aside from all of the revolutionary biology going on (in both senses for which Dick is now famous), seeing who came to visit made me feel very privileged, and piqued my interests: the lab was clearly an organizer of knowledge flows (Dick had multiple approaches and problems in his pot-au-feu). A social and informational network inevitably had filters as well as sensors, so I was intrigued by his visitors, and this stimulated my interest in the social structure of science. Lewontin brought me to the cutting edge in science, and extended new vistas in the philosophy of science, for me, as he has for many other philosophers. The many disciplines he intersected will miss him.

William C. Wimsatt

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