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Other Histories, Other Biologies

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1. Taking the counterfactual turn

When philosophers look to the history of biology, they most often ask about what happened, and how best to describe it. They ask, for instance, whether molecular genetics subsumed the Mendelian genetics preceding it, or whether these two sciences have maintained rather messier relations.[1] Here I wish to pose a question as much about what did not happen as what did. My concern is with the strength of the links between our biological science—our biology—and the particular history which brought that science into being. Would quite different histories have produced roughly the same science? Or, on the contrary, would different histories have produced other, quite different biologies?

I shall not endeavour to address the whole of biology or its history. I will concentrate on genetics, the headline-grabbing branch of biology in our time. The claims of this science on our future have given its history an unusually high public profile. Newspaper articles on the completed Human Genome Project came with timelines of genetic achievement, stretching back into the pre-Mendel mists, and forward to a future where, thanks to genetics-based medicine (we were told), the average person will live to more than ninety. Even more recently, the fiftieth anniversary of the introduction of the double-helix model of DNA in 1953 prompted books, symposia, television programmes, even a cover story in *Time* magazine. It also spurred people to wonder out loud about the nature of history. In 2003, we celebrated James Watson and Francis Crick above all. But they inferred the structure of DNA from Rosalind Franklin's remarkable X-ray crystallographic photograph of the B form of DNA. Might Franklin have given the world the double helix?

Earlier versions of this chapter were presented in 2003 to audiences in Leeds and Dublin as well as in London. I am grateful to all who attended on those occasions. I owe particular debts to my Leeds colleagues for their encouragement and suggestions; to the Royal Institute of Philosophy for the initial invitation; and to Jean Gayon, Jonathan Harwood and Richard Lewontin for helpful comments on a draft.

[1] For a survey of the 'Mendel and molecules' debate, see Kim Sterelny and Paul E. Griffiths, *Sex and Death: An Introduction to Philosophy of Biology* (Chicago: University of Chicago Press, 1999), chs. 6 and 7.

Watson had trained in genetics, Crick in physics. It is tempting to follow Watson himself and ascribe their success to this unique collaboration between different sciences. On this view, the discovery of the double helix awaited the partnering of genetical expertise with X-ray crystallographic expertise. Certainly that is how it happened. But whether it had to happen that way is another matter. A long tradition of counterfactual conjecture to the contrary centres on Franklin. Suppose we could rewind history's tape and keep that photograph out of Watson's hands a little while longer. Unlike Watson, Franklin was no geneticist, and had long thought of DNA as a structural, not a biological, puzzle. But by early 1953, she had given up her long-held prejudices about using structural models and contemplating helices. 'Would it have taken her much longer', asked the distinguished historian of biology Robert Olby, 'to come to the conclusion that the study of the relationship between A and B as helices was the way to go? The answer, though speculative, is surely that it would not.'[2]

Success in science has an air of inevitability about it. Talk of what might have been has an air of speculation about it. This paper aims to show how the critical examination of success in science can make for a less speculative assessment of alternative pasts. The case that will concern me is even more fundamental to our biology than the discovery of the molecular nature of the gene: the discovery of the gene itself. In asking whether we might have had a nongenic biology, I will attempt to illustrate by example just how much evidence from the actual past can be brought to bear on conjectures about possible pasts. Much of what follows will be history filtered through philosophy. At the outset, however, some philosophy leavened with history will help clarify what is, and is not, at stake.

2. The meaning of success

The success of our biology is a thing of wonder. No doubt it holds important lessons about our world and about ourselves. But what lessons? A naïve answer at least has the virtue of clarity. Consider, as an opening bid, that biological success shows (1) that we have got the world about right; and (2) that we could not help but get the world right eventually. More schematically:

[2] Robert Olby, 'Rosy Revised', *London Review of Books* (20 March 2003), 15.

(1) The basic entities, processes and events referred to in our best-confirmed biological theories really exist or occurred; and
(2) The inclusion of those entities, processes and events was inevitable.

Although I shall here be concerned mainly with (2), and then as it applies to just one basic entity, the gene, it is well to begin by noticing that there are several ways of connecting the realism expressed in (1) with the inevitabilism expressed in (2).[3]

The naïve view sketched above holds realism and inevitabilism to be mutually supporting. The items inventoried in our biology are inevitable because they are real, and the existence of these items guarantees their inclusion in a mature biology. So, says the realist-inevitabilist, the inclusion of the gene was inevitable because genes really exist, with something like the properties ascribed to them, and no serious, unhindered attempt to investigate life on Earth could have failed at some point to bump up against them and accord them basic status. But why should we believe that genes are real in the first place? The realist-inevitabilist will appeal in part to historical considerations—in the case of genes, to one of the most famous episodes of simultaneous discovery in the whole of science. As textbooks still proclaim, around 1900, three European botanists, Hugo de Vries, Carl Correns and Erich von Tschermak, independently rediscovered Gregor Mendel's principles of heredity, thus laying the conceptual foundations for genetics.

On the naïve view, the triple rediscovery reveals that, once background knowledge was sufficiently advanced, recognition of the gene was inevitable. The gene forced itself into our theories the moment we were ready to receive it. Mendelism was thus not of our making; and if not for Mendel, and after him De Vries, Correns and Tschermak, then the delivery of the gene would have fallen to others. Contemplating Mendel's long neglect and sudden, multiple rediscovery inspired the anthropologist Alfred Kroeber, writing around 1920, to clumsy eloquence:

> There may be those who see in these pulsing events only a meaningless play of capricious fortuitousness; but there will be others to whom they reveal a glimpse of a great and inspiring inevitability which rises as far above the accidents of personality

[3] This analysis fleshes out the remarks on success, realism and inevitabilism in Ian Hacking, *The Social Construction of What?* (Cambridge, MA: Harvard University Press, 1999), ch. 3, esp. 68-70, 78–80.

> as the march of the heavens transcends the wavering contacts of random footprints of clouds on earth. Wipe out the perception of De Vries, Correns, and Tschermak, and it is yet clear that before another year had rolled around, the principles of Mendelian heredity would have been proclaimed to an according world, and by six rather than three discerning minds.[4]

What of those who see in the early history of Mendelism but 'a meaningless play of capricious fortuitousness'? The converse of the naïve, realist-inevitabilist view links scepticism about the existence of genes (antirealism) with scepticism about the inevitability of their inclusion in biological theory (contingentism). Yes, it is conceded, if genes existed, then modern biology would have been bound to include them at some point. But there are reasons, independent of historical considerations, for thinking that genes, as conventionally conceived, do not exist. It follows that if genes are not there in the world to be bumped up against, they cannot be held responsible for the emergence of a scientific consensus in favour of their reality. Where such a consensus holds, it owes its origins and maintenance instead to the contingencies of local history. Within our biological sciences, an unlikely chain of events at the beginning of the century led to belief in genes becoming entrenched while other, rival beliefs, no less well evidenced, went extinct. Since then, admittedly, the idea of the gene has turned out to be a productive one for framing many of our inquiries. But the history of science is strewn with false, useful beliefs (phlogiston, ether). Furthermore, the biological sciences might well have done equally well, or better, within a nongenic framework.

These contrary positions—on the one side, realism-inevitabilism; on the other, antirealism-contingentism—by no means exhaust the possibilities. Swapping the left-hand isms for each other generates two more worth considering. There is, first, antirealism-inevitabilism. By its lights, while belief in genes is unwarranted, the idea of the gene is nevertheless inescapable, once biological inquiry, wherever and whenever begun, has developed to a certain pitch. Gene theory here is seen as a necessary passage point to the future, a gate through which a scientific community must travel if it is to remain successful, not because genes exist—that is something science can never settle—but because human knowledge has a

[4] Alfred Kroeber, 'The Superorganic' (1917), revised 1927 version, reprinted in *Frontiers of Anthropology*, Ashley Montagu (ed.) (New York: Capricorn Books/G. P. Putnam's Sons, 1974), 344–81, quotation on 372–73. The text here reads 'on clouds of earth', which, given the sense of the passage, I take to be a mistake.

certain logic of development. The guiding spirit here is Auguste Comte's, for Comte regarded the postulation of unobservable entities as an unavoidable waystation in the growth of inquiry, marking out a middle, metaphysical stage from an earlier, theological one and a later, culminating, positivist one.

The Comtean has confidence in history. By contrast, the realist-contingentist—occupant of the final position in this quartet—regards history with suspicion. Yes, genes are real, but, says the realist-contingentist, that does not mean their discovery and acceptance was inevitable. If not for past events that could well have turned out differently, we might never have found our way to genes, and our biological sciences would now be nongenic. Maybe this ignorance of genes would have been hobbling, and we would now struggle to understand and control our world much more than we do. But then again, maybe, with genes out of the running, we would have embraced some other, now unknown, but equally real and serviceable entity as basic to our notions of heredity.

I hope the above suffices to suggest that the question of inevitability arises independently of the question of realism. No matter what you think about the ontology of genes, there is room for asking about the inevitability of the idea of the gene within the modern biological sciences. This is not to say that realism and inevitability can be cleanly bracketed off from one another, however. We shall see that they cannot. Moreover, the four positions I have sketched are not equally attractive. The latter two are, for most tastes, decidedly exotic. That leaves the naïve view and its converse, respectively yoking realism to inevitabilism, and antirealism to contingentism. Someone swayed by, say, Evelyn Fox Keller's argument that our biological sciences have outgrown the concept of the gene, and would be better off without it, will probably be inclined to accept a larger role for contingency in the initial canonization of that concept than someone not so swayed.[5] As ever, where logic fears to tread, psychology rushes in.

3. Multiple discovery and gene inevitabilism: the Mendelian convergence

Was a genic biology inevitable? We require well-developed arguments for and against for evaluation. But that is not where we

[5] Evelyn Fox Keller, *The Century of the Gene* (Cambridge, MA: Harvard University Press, 2000). For ontological discussion in a similarly iconoclastic spirit, see John Dupré's chapter in this volume.

stand. The weight of presumption has traditionally come down so much on the side of gene inevitabilism, or on the side of pessimism about counterfactual inquiry (for who can know what might have been?), that gene contingentism has hardly had a look. The main burden of this paper is to shift some of the barriers confronting the gene contingentist at the start.

Let us return, first, to the rediscovery of Mendelism in 1900 as an instance of independent convergence on the genic truth. To the extent that De Vries, Correns and Tschermak arrived at the same conclusions in isolation from each other, and from Mendel, the principles of Mendelian heredity can indeed, as Kroeber suggested, be judged as independent of the precise historical circumstances that carried them into scientific consensus. Note that convergence thus offers, at least in principle, and contrary to global counterfactual pessimism, a straightforward empirical test of inevitability. The greater the number of past trajectories that converged on the same conclusion, and the greater the independence of those trajectories, the more plausible will be the idea that the conclusion was inevitable. Kroeber indeed laid great store by convergence, piling up famous examples of multiple, simultaneous discovery alongside the Mendelian one: Leibniz and Newton converging on the calculus; Darwin and Wallace on evolution by natural selection; and so on. He took it that the best explanation for so much convergence was the inevitability of a discovery or invention, given the accumulation of human knowledge to a certain threshold.[6]

The convergence argument for inevitabilism was not new to Kroeber. It can be found, for instance, nearly a century earlier, in the English historian Macaulay's reflections on science and art.[7] Strikingly, it has become well known in our own time less as an historical argument about the nature of biology than as a biological argument about the nature of history. I refer to the well-known debate between the palaeontologists Simon Conway Morris and the late Stephen Jay Gould. In the contingentist camp is Gould,

[6] Op. cit. note 4, 369–75. On Kroeber's larger purposes in this influential paper, see Abram Kardiner and Edward Preble, *They Studied Man* (New York: Mentor, 1963), 169–72.

[7] For Macaulay, and citations to other instances of the argument from multiple discovery to inevitability, see Robert K. Merton, 'Singletons and Multiples in Science' (1961), reprinted in his *The Sociology of Science: Theoretical and Empirical Investigations*, N. W. Storer (ed.) (Chicago: University of Chicago Press, 1973), ch. 16, 353–4.

arguing that modern animals might well have evolved radically different anatomies, had contingent events at the end of the Cambrian era resulted in a different selection of survivors. In the inevitabilist camp is Conway Morris, arguing that, whatever happened in the Cambrian era, modern animals would look broadly similar to the animals that now inhabit Earth, since natural selection optimizes anatomical design, and the set of optimal designs is narrow. The ace up Conway Morris' sleeve is convergence: over and over again, it seems, independent lineages have evolved the same designs—eyes, wings, fishiness, intelligence, social organization, and so on.[8]

For the inevitabilist, then, much depends on establishing that two or more convergent pathways were in fact independent. Otherwise, the spectre arises of convergence due to the contingent sharing of a local, constraining inheritance. That spectre often proves harder to exorcise than the inevitabilist might hope. Certainly the convergence argument for gene inevitabilism now looks decidedly shaky. Superb historical detective work has revealed the triple rediscovery of Mendelism to be a far more tangled affair than Kroeber supposed. The whole idea that Mendelism amounts to a rediscovery now looks problematic. For one thing, the monk in the garden did not, it seems, regard his work as revolutionizing the science of heredity. Rather, he offered his discovery of a constant, three-to-one ratio of characters in the offspring of hybrid pea plants, and his explanation for this and related ratios, as interesting conclusions salvaged from a failed attempt to produce new species through hybridization. In explaining the ratios, furthermore, Mendel did not postulate the existence of genes. He did introduce a number of ideas later recognizable as 'Mendelian': that alternative characters, such as yellow versus green seed colours, were either 'dominant' or 'recessive' (his terms); and that in hybrid plants, exhibiting just the dominant character but containing factors for the recessive one too, dominant and recessive factors segregated at random into separate gametes. But for Mendel, these factors were

[8] The best introduction to the debate is Simon Conway Morris and Stephen Jay Gould, 'Showdown on the Burgess Shale', *Natural History* **107** (December 1998—January 1999), 48–55. See also Gould, *Wonderful Life: The Burgess Shale and the Nature of History* (London: Hutchinson Radius, 1989), esp. ch. 5; Conway Morris, *The Crucible of Creation: The Burgess Shale and the Rise of Animals* (Oxford: Oxford University Press, 1998), esp. ch. 8, and *Life's Solution: Inevitable Humans in a Lonely Universe* (Cambridge: Cambridge University Press, 2003).

not stable atoms of heredity, located in cells and retaining their identities through time. They were not, in short, genes.[9]

'Rediscovery' misleads as a name for what happened around 1900, then, in part because Mendelian principles resembled Mendel's conclusions only in a piecemeal and distorted way. But the fit is even more awkward. There is now little doubt that De Vries, Correns and Tschermak were all aware of Mendel's paper at earlier stages in their research than they later said. The contribution of De Vries, who published first, was arguably the most dependent on a reading of Mendel, for the great Dutch botanist seems to have hit neither on the ratios nor on their explanation independently. Correns does appear to have completed the bulk of his hybridization research before searching the literature and finding the 1866 paper. But he was a former student of Mendel's botanical correspondent Karl von Nägeli, so a prior influence cannot be ruled out. Moreover, the slow gestation of Correns' own paper may well be a sign that the late reading of Mendel brought new clarity. Be that as it may, Correns' trumpeting of Mendel's priority in discovery was probably intended less to bestow honour on Mendel than to take it away from De Vries, an envied rival. (As Correns pointed out, De Vries in his initial paper had quietly abandoned his own vocabulary for Mendel's, though not mentioning Mendel at all.) Tschermak, it seems, did discern the ratios independently of Mendel, but made little of them until he noticed the Mendelian bandwagon starting to roll, then clambered on.[10]

Some mention should be made as well of the small to non-existent roles that De Vries, Correns and Tschermak went on to play in establishing Mendelism as the basis for a new science of heredity. That fell largely to others, notably the Cambridge

[9] The revisionist scholarship on Mendel is summarized in Peter J. Bowler, *The Mendelian Revolution: The Emergence of Hereditarian Concepts in Modern Science and Society* (Baltimore: Johns Hopkins University Press, 1989), ch. 5. An excellent web resource on Mendel and Mendelism, including an annotated translation of the 1866 paper, is MendelWeb; see http://www.mendelweb.org (accessed July 2004).

[10] On 'rediscovery' as an inadequate label for what happened to Mendel's work around 1900, see Robert Olby, 'Rediscovery as an Historical Concept', *New Trends in the History of Science*, R. P. W. Visser *et al.* (eds.) (Amsterdam: Rodopi, 1989), 197–208. See also the more detailed discussion in his *Origins of Mendelism*, 2nd edition (Chicago: University of Chicago Press, 1985), ch. 6. The personal dimension is nicely captured in Robin Marantz Henig, *The Monk in the Garden* (New York: Houghton Mifflin, 2000), chs. 14 and 15.

zoologist William Bateson, of whom more below. For our purposes, the point is that neither independence nor convergence is straightforwardly assessed. We quickly find ourselves asking what criteria have to be met for different historical trajectories to count as independently convergent. How similar do they need to be, in what respects, and why? Other putative cases of independent convergence present similar difficulties. Consider those 'co-discoverers' of evolution by natural selection, Darwin and Wallace. They were different from each other in all sorts of interesting ways. But they shared much as well, including ideas generative of their evolutionary theories, notably the Malthusian population principle and the Lyellian view that history explains biogeography. Even if one overlooks the common inheritances, intellectual and cultural, there remains the fact that Wallace's theory was not strictly identical to Darwin's.[11] On what grounds shall they be declared the 'same' theory? Moving from the history of biology to biology itself, consider the emergence of eyes in animal lineages constituting distant branches of the evolutionary tree. Eyes can be found among the vertebrates, arthropods and molluscs, but not among their common ancestors. Yet, in each phylum, the development of eyes is regulated—so our genic biology teaches—by genes similar enough to work when swapped into organisms belonging to the other phyla. Those eyeless ancestors seem thus to have bequeathed, not eyes, but the biochemical apparatus making eyes possible.[12]

Whatever the general status of convergence arguments for inevitabilism, the convergence argument for gene inevitabilism is wanting. That argument is, however, but one that might be raised against gene contingentism. In the remainder of the paper I shall address three more objections. First, I shall consider whether the failure of Lysenkoism—a nongenic biology that flourished in the mid-twentieth-century Soviet Union—can be counted as an instance of punished divergence from the genic truth. I shall then

[11] On whether Darwin and Wallace converged independently on natural selection, see Gregory Radick, 'Is the Theory of Natural Selection Independent of its History?', *The Cambridge Companion to Darwin*, Jonathan Hodge and Gregory Radick (eds.) (Cambridge: Cambridge University Press, 2003), ch. 6, 149–50.

[12] On convergence and the eye, see Stephen Jay Gould, *Leonardo's Mountain of Clams and the Diet of Worms* (London: Vintage, 1999), ch. 17, 331–2; cf. Simon Conway Morris, *Life's Solution*, op. cit. note 8, 151–73, 193. On the large scope for disagreement about claims for convergence in biology, see Adrian Woolfson's review of the latter, 'How to Make a Mermaid', *London Review of Books* (5 February 2004), 25–6.

turn to the question of whether, around 1900, there were serious alternatives to Mendelism that might have served equally well as a basis for a new science of heredity. I shall make a preliminary case for Galtonian biometry, especially as developed by W. F. R. Weldon, as just such an alternative. Finally, I will consider a challenge that puts a new, counterfactualist spin on the familiar topics of theory incommensurability and the theory-ladenness of observations. The worry here is that an intuitively attractive strategy for demonstrating that a losing theory could have been a winner is in fact incoherent.

4. Abandoned alternatives and gene inevitabilism: the Lysenkoist divergence

The twentieth century contains at least one famous and amply documented example of a nongenic biology: Lysenkoism. It ran in parallel with genic biology through the middle decades of the century. It enjoyed enviable institutional clout. Its practitioners took a robustly sceptical stance toward the existence of genes. And it was, by common consent, an utter fiasco. On the face of it, then, the failure of Lysenkoism argues against gene contingentism and for gene inevitabilism. It seems to show that no scientific community deserving of the name can ignore the gene forever. The challenge before the gene contingentist is thus to explain why this is not the right lesson to draw from Lysenkoist failure. But first, a brief review of Lysenkoism is in order.

The movement took its name from the Soviet agrobiologist Trofim D. Lysenko, who in 1936 put his doubts about the gene plainly. What 'we deny', he said, was 'that the geneticists and the cytologists will see genes under the microscope.' Microscopic studies, Lysenko continued, will no doubt reveal structures of interest; but these 'will be particles of the cells, nuclei or chromosomes, and not what the geneticists mean by genes.' In Lysenko's view, the fundamental mistake of 'Mendelism-Morganism' was the notion that heredity could be identified with a mere part of the organism—a bit of chromosome, if T. H. Morgan's school of fruitfly geneticists were to be believed—rather than the whole set of an organism's ever-changing relations with its environment. More perniciously, as Lysenko saw it, the geneticists' false theory of heredity drew support from, and lent support to, a related doctrine: that acquired characters could not be inherited. A major Lysenkoist ambition was to show, on the contrary, that permanent improvements to crop varieties could be engineered through directed transformations of the environment. These views were much debated in the Soviet Union in the 1930s to the mid-1940s. But by the late 1940s, Lysenkoism had won monopoly rights as the Soviet science of heredity. Mendelian genetics was shut down, its leaders marginalized, even imprisoned.[13]

There is a well-known ideological dimension. Although the Bolsheviks had supported genetics from early days, Lysenko gradually tarred it with the brush of elitist, mystifying reaction. Where, according to Lysenko, the revolution needed energetic guidance on rational breeding, the academic geneticists taught that breeders could do nothing but await fortuitous mutations. 'Mendelism-Morganism is built entirely on chance', declared Lysenko, in a notorious 1948 address. 'There is no effectiveness in such science. With such a science it is impossible to plan, to work toward a definite goal; it rules out scientific prediction.' The political credentials of Mendelism-Morganism were little helped by its class affiliation. Unlike Lysenko, the son of peasants, the geneticists came overwhelmingly from bourgeois backgrounds. A further liability was the association with lab-bound fruitflies. As symbols for the otherworldly sterility of academic genetics, flies were second to none. A cartoon from the Soviet periodical press of the era shows a geneticist, pockets full of test tubes of fruit flies, marching arm in arm with a Klansman and a policeman. Another has a fat-cat businessman admiring the flies which, the Lysenkoists alleged, had distracted Soviet scientists from the task of improving agriculture. The geneticists had wanted to learn about flies when the people had needed them to learn about wheat.[14]

[13] For Lysenko in his own words, and in English, the indispensable volume is T. D. Lysenko, *Agrobiology: Essays on Problems of Genetics, Plant Breeding and Seed Growing* (Moscow: Foreign Languages Publishing House, 1954). The quotation is from 'Two Trends in Genetics' (1936–7), 160–94, 186. The whine of axes grinding is never far off in the historiography of Lysenkoism. For a non-Marxist perspective, see David Joravsky, *The Lysenko Affair* (Cambridge, MA: Harvard University Press, 1970). For a Marxist but not uncritical perspective, see Richard Levins and Richard Lewontin, 'The Problem of Lysenkoism' (1976), in their *The Dialectical Biologist* (Cambridge, MA: Harvard University Press, 1985), ch. 7.

[14] The quotation is in T. D. Lysenko, 'The Situation in Biological Science' (1948), in his *Agrobiology*, op. cit. note 13, 515–54, 552. For the cartoons, illustrating a 1949 article entitled 'Fly-Lovers and Man-Haters', see Valery N. Soyfer, *Lysenko and the Tragedy of Soviet Science*, L. and R. Gruliow (trans.) (New Brunswick, NJ: Rutgers University Press, 1994), illustration insert, no. 19.

Yet, for all its ideological correctness, Lysenkoism at last fell from favour. Why? According to one of the most senior Western historians of Soviet science, Loren Graham, the Soviets had a belated reality check. He suggests that, as the theoretical and practical failures of the Lysenkoists mounted, and as the excuses for failure became less and less convincing, it became obvious that, to put it bluntly, Lysenkoism was wrong. The abandonment of Lysenkoism thus shows that science is a social construction only within certain bounds. Even totalitarian societies cannot pursue congenial but false sciences forever. Graham compares the Soviets' denial of the realities of the marketplace to their denial of the realities of the gene. 'Despite all the social constructivist support' for Lysenkoist biology and Marxist economics, he argues, 'both have fallen into eclipse. Both the gene and the market have reemerged, and, one is tempted to add, "with a vengeance." Natural and economic realities have obtruded.' Graham lingers especially over the famous image of Khrushchev visiting an Iowa farm in the early 1960s, amazed to learn of its productivity, and of the Mendelian principles that, as Khrushchev was told, guided the development of the American agricultural wonder, hybrid corn.[15]

On Graham's reading, then, the failure of Lysenkoism is a kind of divergence argument for gene inevitabilism. Eventually, he suggests, a path of inquiry angled away from the gene becomes intolerably steep. Under Lysenkoism, the ignored genes wreaked their vengeance through Soviet agriculture, leaving it enfeebled compared with gene-savvy American agriculture. The message borne home to Khrushchev—that, in Graham's gloss, Western genetics had developed 'much more effective agricultural practices than Lysenko's genetics'—amounts, for Graham, 'to the intrusion of reality into Lysenko's socially constructed worldview.' No player of favourites, reality would, it seems, have intruded just as rudely in the Western market economies if Mendelian genetics had somehow failed to find its footing there in the early twentieth century. The greater success of American versus Soviet agriculture at mid-century thus appears to count against gene contingentism.[16]

Is the testimony of agriculture indeed so unequivocal? The legacies of the Cold War are such that, even now, one needs to consult the Marxists for a contrary view. The case for doubt has been put most effectively by the self-described 'dialectical biologist'

[15] Loren R. Graham, *What Have We Learned About Science and Technology from the Russian Experience*? (Stanford: Stanford University Press, 1998), 17–31, quotation on 31.

[16] Graham, op. cit. note 15, quotation on 25.

Richard Lewontin and his colleagues. Their arguments have not, to my knowledge, been answered. Graham does not even acknowledge them. Here are four of the most impressive in the Lewontonian brief. First, comparative data on annual crop yields from the 1920s to 1960s, far from showing the damaging effects of Lysenkoism, reveal roughly similar rates of gain in yield in the Soviet Union as in the United States—perhaps because better machinery and chemicals, common to farming in both nations, mattered much more than divergent theories of inheritance. Second, the rejection of Lysenkoism should be seen as part of a wider generational shift in the Soviet Union, as the idealist revolutionaries, willing to bear the costs of establishing a socialist alternative, gave way to pragmatic bureaucrats unwilling to bear those costs. Third, the famous Mendelian agricultural success story, hybrid corn, is not universally more productive. It does best under the conditions of soil and climate which characterize the American corn belt. Under other conditions, whether in the US or in the former USSR (which has a tiny corn belt), local corn varieties do better. Fourth, there is room to doubt that only Mendelism can guide the breeding of corn as productive (*ceteris paribus*) as hybrid corn. Horticulturalists might well have achieved as much using pre-Mendelian methods, selectively crossing the highest-yield individuals from the highest-yield variety, generation after generation. The attraction of Mendelism for American seedsmen was not its promise of otherwise unattainable yields, but the prospect of forcing farmers to return to the seedsmen year after year (since plants born of seeds produced through Mendel-style, intervarietal hybridization would not themselves breed true).[17]

Each of these points applies pressure to the presumption that theories of inheritance, correct or incorrect, on either side of the former Iron Curtain, have had much to do with the practice of agriculture. Here are historical and scientific grounds on which to hesitate before concluding, with Graham and others, that agricultural reality crushed a would-be rival to genic biology. Even so, there are other, conceptual grounds for distinguishing the actual fate of Lysenkoism from the possible fates of nongenic biologies. As we have seen, Lysenkoism was not defined solely by a negative doctrine, the non-existence of genes. There were a number of positive doctrines, most famously a belief in the 'Lamarckian' inheritance of acquired characters. There were also less well-

[17] See Levins and Lewontin, op. cit. note 13, esp. 171–4, 188–191, and Jean-Pierre Berlan and R. C. Lewontin, 'The Political Economy of Hybrid Corn', *Monthly Review* **38** (July-August 1986), 35–47.

defined but no less characteristic attitudes, such as the emphases on process over structure, on the environmental situation of the organism, and on the need to study problems which bore directly on agricultural concerns. None of these positive doctrines and attitudes are deductively entailed by scepticism about the existence of genes. Moreover, all of them, especially the Lamarckism, mark Lysenkoist biology off from current biology. For purposes of counterfactual testing of gene scepticism, at least at the first step, we need to do away as much as possible with such complications. What we require is something as much like Mendelian genetics as possible, except without the genes. One promising candidate is Weldonian biometry.

5. Weldonian biometry as a plausible competitor to Mendelian genetics

Born the same year as Mendel (1822), Francis Galton is now most often recalled, indeed reviled, as the begetter of the rational management of human breeding, or what he called 'eugenics'. But eugenics was just one facet of a remarkably creative, diverse and influential scientific enterprise, stretching from the 1850s into the 1900s. In his own lifetime, Galton's ideas about controlling heredity had less impact than his ideas about how to study it and how it worked. He inaugurated the analysis of human pedigree data and the study of twins as means for disentangling nature from nurture. He conducted careful experiments to test his cousin Charles Darwin's theory of inheritance, pangenesis. He developed his own theories on the physiology of inheritance.[18] But what most impressed the biologists and anthropologists who came of professional age in the 1890s was the programme, set out most fully in Galton's 1889 book *Natural Inheritance*, for the statistical study of inheritance at the level of the population. This was 'biometry'; and in the hands of its leading practitioners and propagandists, the mathematician Karl Pearson and, especially, the zoologist W. F. R. Weldon, it came to stand for a well-defined set of means, ends and objects of study.[19]

[18] An excellent study of Galton in the round is Nicholas Wright Gillham, *A Life of Sir Francis Galton: From African Exploration to the Birth of Eugenics* (Oxford: Oxford University Press, 2001). Like Mendel, Galton is well served on the web; an especially generous selection of Galtoniana is available at http://www.mugu.com/galton/ (accessed July 2004).

[19] Francis Galton, *Natural Inheritance* (London: Macmillan, 1889). On this book and its role in fostering biometry, see Gillham, op. cit. note 18, chs. 18 and 19.

A good number of these are visible in a collaborative paper of 1893, regarded as exemplary in its own day. (How far the exemplar was, in one or another of Kuhn's senses, paradigmatic, is a matter I shall consider below.) Under scrutiny were measurements of eleven anatomical characters in adult female shore crabs—carapace breadth and so on—from two different populations or 'races', one living in Plymouth Sound, the other in the Bay of Naples. The mathematical sifting of this data revealed what were, for Weldon and Pearson, three major prizes. First, the measurement sets almost all distributed themselves into bell-shaped curves. Second, the sole exception resolved itself, on further analysis, into two separate bell-shaped curves, revealing dimorphism for that character in that population. Third, variation in some features correlated with variation in other features in numerically precise ways. (The now-standard statistical concept of correlation was Galton's invention, as was the concept of regression.) Taken as a model, the paper thus commended attention, first and foremost, to statistical regularities among continuously varying characters in large natural populations.[20]

Biometry so construed was not so much a theory of inheritance as a cluster of methodological preferences. In the late 1890s, however, a theory of inheritance precipitated out as well, around what Pearson dubbed Galton's Law of Ancestral Heredity. Galton introduced the law formally in 1897, though its origins can be traced back much further in his writings.[21] Weldon later stated it thus: 'that the two parents contribute between themselves one-half of the total heritage of the offspring, that the four grandparents contribute one-quarter, the eight great-grandparents one-eighth, and so on. Thus the sum of the ancestral contributions is expressed by the series (1/2 + 1/4 + 1/8 + 1/16 + ...), which, being equal to 1, expresses the whole heritage.'[22] What, precisely, was being added up here was

[20] W. F. R. Weldon, 'On Certain Correlated Variations in *Carcinus moenas*', *Proceedings of the Royal Society of London* **54** (1893), 318–29. On this paper, and Pearson's contribution to it, see Gillham, op. cit. note 18, 281–3, and Jean Gayon, *Darwinism's Struggle for Survival: Heredity and the Hypothesis of Natural Selection*, M. Cobb (trans.) (Cambridge: Cambridge University Press, 1998), 204–10.

[21] Francis Galton, 'The Average Contribution of Each Several Ancestor to the Total Heritage of the Offspring', *Proceedings of the Royal Society of London* **61** (1897), 401–13, and 'A Diagram of Heredity', *Nature* **57** (1898), 293. On the law as Galton conceived it, see the superb discussion in Gayon, op. cit. note 20, 132–46.

[22] [W. F. R. Weldon], 'Current Theories of the Hereditary Process' (eighth lecture), *The Lancet* (25 March 1905), 810.

never fully settled. Galton was happy for the formula to apply sometimes to a single individual, and at other times to a whole generation. Pearson judged these conceptions to be inconsistent, however, and introduced a series of modifications aimed at bolstering the law as a predictor of characters in the individual (the law's proper domain, he thought). Through all the debate, the core 'ancestrian' intuition nevertheless remained intact: the hereditary contribution of an ancestor to descendants suffers regular diminution with each generation, but, as a rule, is never extinguished.[23]

A thorough positivist, Pearson felt there was no need to make physiological sense of the law, so long as it successfully predicted what was observed; and this attenuated version of biometry has tended to be best remembered. But Galton's thinking was quite otherwise, as was Weldon's.[24] At the start of a series of lectures on inheritance, presented in London in 1904–5, Weldon—by far the most expert biologist at the biometrical vanguard—argued that while statistical facts were the proper data of a science of heredity, 'when an explanation was sought of the mechanism or *modus operandi* of heredity, one passed ... outside the domain of statistics and concrete facts and had to picture the invisible organic processes accompanying the growth and the reproduction of animals.'[25] Weldon's own picture of those processes remained

[23] Pearson reviewed the changes in Karl Pearson, 'A Mendelian's View of the Law of Ancestral Inheritance', *Biometrika* **3** (1904), 109–12. On Pearson's interpretations of Galton's law, see Michael Bulmer, 'Galton's Theory of Ancestral Inheritance', *A Century of Mendelism in Human Genetics*, M. Keynes, A. W. F. Edwards and R. Peel (eds.) (London: Galton Institute/CRC Press, 2004), 13–18, esp. 15–16, and, more extensively, Bernard J. Norton, *Karl Pearson and the Galtonian Tradition: Studies in the Rise of Quantitative Social Biology* (unpublished Ph.D. dissertation, UCL, 1979), ch. 6.

[24] Pearson was of course the author of that influential positivist breviary, *The Grammar of Science* (London: Scott, 1892). In Galton's 1897 paper introducing the law, he had argued that 'its close agreement with physiological phenomena'—in particular, the halving of the germinal material in the production of gametes—'ought to give a prejudice in *favour* of its truth.' Galton, op. cit. note 21, 403, emphasis in original. For Pearson, however, the law, as he wrote in 1903, 'is not a biological hypothesis at all, it is simply the statement of a fundamental theorem in the statistical theory of multiple correlation applied to a particular type of statistics.' Karl Pearson, 'The Law of Ancestral Heredity', *Biometrika* **2** (1903), 211–29, quotation on 226.

[25] The abstracts of Weldon's lectures on 'Current Theories of the Hereditary Process' appeared in *The Lancet* (1905), 42, 180, 307–8, 512, 584–5, 657, 732, 810. The quotation is from 42.

tragically incomplete: he died unexpectedly in 1906, at the age of forty-six, while at work on a book on inheritance. The outlines can nevertheless be made out clearly enough. Roughly, in Weldon's view, what an individual inherited was a set of 'determinants', themselves—in higher animals—constituents of the chromosomes. 'Determinant' sometimes went in quotes for Weldon, to indicate that this term was common among students of inheritance, but also perhaps because he emphatically did not think of germinal causes as acting independently of context. He insisted on the influence of the chemical and physical environments on the form of hereditary characters. He also envisaged a kind of contest among the chromosomal determinants. In general, the more active or vigorous an individual determinant, the greater its share in the character. At the extreme, one determinant could dominate wholly.[26]

Weldon's early death cut short the most promising interpretative effort on behalf of ancestrian biometry. It also, and rather more famously, brought to an end the most formidable resistance to Mendelian genetics in its early days. The shape of the 'biometrician-Mendelian' controversy, pitting Weldon, Pearson and their biometrical allies against Bateson and his Mendelian allies, is well known, as are some of the explanations historians have offered for its bitterness. These need not detain us here.[27] What matters for our purposes is that there were issues of substance in dispute—issues that might well have been decided in another way.

No less than ancestrian biometry, Mendelism was a theory of inheritance and a set of beliefs about how it ought to be studied. Aspects of both ran against the biometrical grain. Theoretically, a major point of contention concerned the gametes of hybrids in

[26] Weldon's 'Theory of Inheritance' and other unpublished writings are contained in the Pearson Papers, 264/2, UCL. For discussion of these and other sources, see Robert Olby, 'The Dimensions of Scientific Controversy: The Biometric-Mendelian Debate', *British Journal for the History of Science* **22** (1988), 299–320, esp. 314–7. See also Norton, op. cit. note 23, 190–3, 218–20. The fullest treatment of Weldon's life and thought remains Pearson's long obituary notice, in *Biometrika* **5** (1906), 1–52. For Pearson's reconstruction of Weldon's theory, see Karl Pearson, 'On a Mathematical Theory of Determinantal Inheritance, from Suggestions and Notes of the Late W. F. R. Weldon', *Biometrika* **6** (1908), 80–93.

[27] The historiography of this debate up to the mid-1980s is summarized in Olby, op. cit. note 26, 300–4. Notable contributions since then include Gayon, op. cit. note 20, ch. 8, and Eileen Magnello, 'The Reception of Mendelism by the Biometricians and the Early Mendelians (1899–1909)', in *A Century of Mendelism in Human Genetics*, op. cit. note 23, 19–32, which makes use of some of Weldon's unpublished letters.

Mendelian crosses. Mendelian theory predicted that hybrids produced equal numbers of gametes of two kinds. Half the gametes determined one form of a character—the form exhibited by one of the hybrid's pure-bred parents. The other half determined the form exhibited by the other parent. Individual gametes thus carried no legacy of the hybrid state of the organism issuing them, but were 'pure' in respect of the parental forms. Bateson and Weldon agreed both that this 'doctrine of gametic purity' was fundamental to Mendelian theory, and that it represented a departure from the Galtonian tradition, since it predicted that ancestral influence could go to zero very rapidly.[28] The difference was clearest in the predictions the two theories made about 'extracted recessives': the organisms comprising the 1 in the Mendelian 3:1 ratio—the green-seeded pea plants born to yellow-seeded hybrid plants. If inbred, extracted recessives should, on Mendelian theory, yield generation after generation of organisms showing the same, recessive character. The reappearance of the old dominant character—an atavism—has to be put down to accident (mutation) or initial impurity. In Weldonian theory, by contrast, the vast majority of individuals among the extracted recessives were expected to harbour the dominant-character determinant. Weldonian theory thus predicted the dominant form of the character to reappear if inbreeding were kept up in such a lineage.[29]

The accompanying differences in method, although less clear-cut than the differences in theory and prediction, are no less striking. The exemplary investigation in the Mendelian tradition was of

[28] Bateson presented gametic purity as the 'essence' of Mendelism in his polemical *Mendel's Principles of Heredity: A Defence* (Cambridge: Cambridge University Press, 1902), quotation on 115. On 'the Mendelian doctrine of gametic purity' as irreconcilable 'with the vast body of facts and data of heredity in human families and races collected and published by Francis Galton and Karl Pearson', see [Weldon], 'Current Theories of the Hereditary Process', op. cit. note 25, 732. Weldon took care to attribute the doctrine to the Mendelians, not to Mendel; see W. F. R. Weldon, 'Mr Bateson's Revisions of Mendel's Theory of Heredity', *Biometrika* **2** (1903), 286–98; esp. 288–9.

[29] For Weldon's derivation of the Mendelian ratio without the assumption of gametic purity, see Norton, op. cit. note 23, 190–3, which presents in more accessible form part of the discussion in Pearson, 'On a Mathematical Theory of Determinantal Inheritance', op. cit. note 26. As Pearson summarized (93): 'We see that Mendelian dominance and the Mendelian quarter may arise in cases where there is no pure gamete, and that the discovery of a latent character may need several generations of breeding.'

course Mendel's own: the experimental hybridizing of distinct varieties, carried through for several generations. The Weldon-Pearson biometrical exemplar offered at least three contrasts. First, the Mendelian began not with continuously varying characters, but with those characters that come in just two forms. Second, the Mendelian tracked those characters not in large, randomly interbreeding populations, but in single lineages born of the selective mating of individuals themselves produced through selective mating. Third, the Mendelian was indifferent to the ancestry of the first, parental generation in a hybridization experiment. It did not matter whether a lineage had been breeding true for twelve generations or two generations. All that mattered was that it bred true. Here, Weldon argued, was a methodological upshot of the doctrine of gametic purity. 'The fundamental mistake which vitiates all work based upon Mendel's method is the neglect of ancestry', he wrote in a famous 1902 critique.[30] 'This neglect of ancestry, the tendency to regard offspring as resembling their parents rather than their race, accounts for much of the apparent inconsistency between the results obtained by different observers who have crossed plants or animals.'[31]

The success of Mendelism over biometry was not total, of course. From very early on, there were demonstrations showing the possibility of Mendelizing characters which varied continuously, so long as one assumed that lots of Mendelian genes of small effect governed a character.[32] Biometry was accordingly made Mendelism-friendly over the first decades of the twentieth century. There remained, and still remain, textbooks on biometry, journals of biometry, departments of biometry, learned people who identify themselves with pride as 'biometricians'. What did not survive the Mendelian revolution is the law of ancestral heredity as more than a merely statistical tool, associated with scepticism about gametic purity and doubts about the wisdom of founding a science of heredity on alternating characters and hybridization experiments. As a result, we live in world where scientific students of heredity organize their knowledge around qualified Mendelism, rather than qualified biometry. A recent and representative undergraduate

[30] W. F. R. Weldon, 'Mendel's Laws of Alternative Inheritance in Peas', *Biometrika* **1** (1902), 228–54, quotation on 252.

[31] Weldon, op. cit. note 30, 242.

[32] The subsumption of the ancestral law under Mendelism culminated in Ronald Fisher's famous paper, 'The Correlation Between Relatives on the Supposition of Mendelian Inheritance', *Transactions of the Royal Society of Edinburgh* **52** (1918), 399–433. For discussion, see Norton, op. cit. note 23, 220.

genetics textbook, for instance, introduces Mendelian phenomena, peas and all, in the second chapter, with biometric phenomena making an entrance only in chapter sixteen.[33]

Could the biometricians have triumphed over the Mendelians? Mendelian success has tended to obscure several points in biometry's favour. We have seen that biometry and Mendelism offered methods and theories of comparable reach. As Weldon practised it, moreover, biometry had experimental and physiological sides potentially as robust as Mendelism's. Weldon and Pearson, professors at Oxford and UCL respectively, commanded more institutional prestige and resources than Bateson, who for a long period held no university position at Cambridge.[34] On a couple of issues, furthermore—and here we adopt a 'Whiggish' stance for the moment—Weldon was much closer to current consensus than Bateson was. Where Bateson was famously reluctant to accept a role for the chromosomes as the locations of the hereditary determinants, Weldon had no such difficulty. Where Bateson was eager to show that the new understanding of heredity made nonsense of Darwinism, Weldon was a loyal Darwinian, held by some to have furnished the first demonstration of natural selection in the wild. A biometrical triumph, then, far from impeding progress, might have helped it along.[35]

6. Theory-laden data and theory incommensurability revisited[36]

Let us allow that, at Weldon's death, ancestrian biometry had more going for it than is sometimes appreciated, maybe even a lot more. Can we go any further in evaluating its counterfactual credentials?

[33] Daniel L. Hartl and Elizabeth W. Jones, *Genetics: Principles and Analysis*, fourth edition (Boston: Jones and Bartlett, 1998).

[34] As Olby has put it, within zoology, 'Weldon enjoyed *insider* status and Bateson *outsider* status.' Olby, op. cit. note 26, 313, emphasis in original.

[35] On Bateson and chromosomes, see William Coleman, 'Bateson and Chromosomes: Conservative Thought in Science', *Centaurus* **15** (1970), 228–314. On Weldon and chromosomes, see [Weldon], op. cit. note 25, 584–5, 810, and Pearson's remarks in Pearson, 'On a Mathematical Theory of Determinantal Inheritance', op. cit. note 26, 81–82. On Weldon and Bateson's divergent attitudes towards Darwinism and other topics, see Olby, op. cit. note 26.

[36] This section owes much to provocative questions from Jeff Ketland, then at Leeds, and from Richard Gray at TCD.

What other sorts of evidence, if any, might we use to judge whether this body of ideas and practices was capable of sustaining a successful, nongenic biology? One intuitively attractive answer suggests itself. If Weldon had lived, he would surely have continued his efforts at showing how well his own theory of inheritance explained the observations explained differently by Mendelian theory, and also how poorly Mendelian theory coped with observations his theory handled well. Since Weldon's day, of course, the stock of accumulated observations to do with inheritance has grown enormously. We know the successes and failures of Mendelian theory with these observations. Why not pick up where Weldon left off, and see how well Weldonian theory does with the same? The better it does, the better will be our reasons for believing the theory was a casualty of contingent history.

There is, however, a possibly fatal objection to such a strategy. The accumulated observations on inheritance, or anything else for that matter, are not pure reports of how the world really is. The observations are contaminated with the theories of the accumulators—'theory laden', in the jargon. Observers beholden to different theories might well have reported the same events quite differently, noticed different patterns, contrived different experiments, attended to quite different events. The same data would therefore likely not have accumulated under the watch of seriously alternative ideas and practices to the ones we have now. On this view, it is therefore pointless to show how well a failed theory could have dealt with the data as we have it now, since it would never have had to deal with those data. Borrowing from fashionable physics, we can picture rival theories as locked in to data sets which exist only in those histories where one or the other theory is dominant. Rival theories are thus, in a quite literal sense, incommensurable; so far as fit-with-the-data is a criterion for theory choice, there is no common metric to reckon the one against the other.[37]

In fact, some splendid examples of data laden with Mendelian theory lie to hand. The most celebrated instance, among historians of biology at least, comes from laboratory studies of the fruitfly. As Robert Kohler has shown, Morgan and his students did not simply investigate flies as they found them, adhering to decaying bananas in flasks around the lab. Rather, they painstakingly bred flies to

[37] On incommensurability in this sense, see Ian Hacking, 'The Self-Vindication of the Laboratory Sciences', *Science as Practice and Culture*, Andrew Pickering (ed.) (Chicago: University of Chicago Press, 1992), 29–64, see 56–7.

make them ever more suitable candidates for Mendelian studies, systematically eliminating whatever interfered with presumptively Mendelian processes. The results, the lab-standardized fly lineages, were theory-laden scientific objects if ever there were.[38] Another instance is less well known, but especially apposite here: Mendel's own observations of peas. In *Biometrika*, the journal Weldon founded with Pearson to carry their programme forward, Weldon published a remarkable colour plate. It shows the seeds of eighteen peas. We do not see two sorts: either yellow or green. What we see is a continuously varying scale, from green to yellowy-green through to greenish-yellow and then finally yellow. 'If Mendel's statements were universally valid, even among Peas', commented Weldon, 'the characters of the seeds in the numerous hybrid races now existing should fall into one or other of a few definite categories, which should not be connected by intermediate forms.'[39] But this was not what Weldon had found, as he explained:

> In attempting to judge the results of other observers, including those of Mendel himself, I have constantly found it difficult to understand the statements made, because of the vagueness of the terms used to describe shape and colour. In order to make my own statements about colour as intelligible as may be, I selected from a sample of [one hybrid variety] a series of 18 peas, which show, after removal of the seed-coats, a fairly gradual series of transitional colours from a deep green to an orange yellow.[40]

Having called the witness of the peas, Weldon arraigned Mendel on charges of letting his theoretical preferences bias his observations. Of course Mendel had been able to see that some yellow seeds were more greenish than others and vice versa. But, according to Weldon, Mendel's prior ideas about inheritance and its study had precluded his appreciating such variation as at all meaningful. We have already encountered Weldon's diagnosis: Mendelian indifference to the ancestry of the parental peas in experimental crosses. As a result of

[38] See Robert E. Kohler, *Lords of the Fly: Drosophila Genetics and the Experimental Life* (Chicago: University of Chicago Press, 1994), esp. chs. 2 and 3. For discussion, see Gregory Radick, 'Cultures of Evolutionary Biology', *Studies in History and Philosophy of Biological and Biomedical Sciences* **34** (2003), 187–200, 197–8. Little in Kohler's analysis would have been news to the Lysenkoists; see Levins and Lewontin, op. cit. note 13, 181.

[39] Weldon, op. cit. note 30, 244.

[40] Weldon, op. cit. note 30, 245. The plate can be found facing 254.

this indifference, Mendel disregarded deviations in character from the parental types. The yellowy green seeds got categorized under 'green'; the greenish yellow seeds got categorized under 'yellow'; and anything really out of the ordinary probably got filed away under 'exceptional'.[41]

The possibility that Mendelian theory infects the accumulated data on inheritance cannot be brushed aside. Its Mendelism-ladenness need not, however, disqualify that data from a role in credentialing Weldonian theory. As we have seen, concerns to the contrary pivot on whether the ancestrian biometry which might have been would likely have answered to an altogether different data set than the one to which Mendelian genetics answers. If so, then the theories are incommensurable, and there is no using the data belonging to one in order to gauge the potential for success in the other.

Certainly the biometricians and the Mendelians held quite different sorts of investigation as exemplary. In their settled forms, moreover, their theories were mutually exclusive, in the sense that the leading practitioners sought to present what was exemplary for the other as a mere special case. A choice had to be made: either the Mendelian ratios were the results of non-Mendelian, gametically-impure processes which more generally conformed in their effects to the ancestral law, or the ancestral law arose from Mendelian, gametically-pure processes operating under specific conditions.[42] So there was exclusivity of a sort. But this exclusivity falls far short of incommensurability. Yes, Weldon gave Mendel rough treatment about the reality of alternative characters in peas. But Weldon did not assert that alternative characters were a fantasm, unintelligible within the biometrical worldview. Rather, he worked to derive Mendelian ratios from non-Mendelian assumptions. In certain

[41] For Weldon's remarks on Mendel's 'yellow' and 'green', see W. F. R. Weldon, 'On the Ambiguity of Mendel's Categories', *Biometrika* **2** (1902), 44–55. Weldon was the first person to point out that Mendel's published data fit his theories improbably well. See Weldon, op. cit. note 30, 233–5; and for discussion, see Magnello, op. cit. note 27, 22–3.

[42] While it is true, as the sociologist of science Barry Barnes has noted, that 'the biometry-Mendelism controversy' is 'itself a slightly problematic historical construct, with many scientists claiming both affiliations', it would be a mistake to conclude from this that there was no real intellectual conflict between biometry and Mendelism. All combinings of the biometrical and Mendelian perspectives called for choices, changes and/or partitionings of domain. See Barry Barnes, review of Kyung Man Kim's *Explaining Scientific Consensus: The Case of Mendelian Genetics* (1994), in *Isis* **87** (1996), 198–9, quotation on 198.

moods, he even described Mendelism and the ancestral law as complementary (though never in a way that suggested they were equals).[43] And Bateson, for his part—after a brief period where he treated the ancestral law and Mendelism as dividing the phenomena of inheritance between them—was among the first to sketch how a modified Mendelism could account for nature's bell curves.[44]

Earlier I raised the question of whether biometry and Mendelism were rival 'paradigms', in Thomas Kuhn's terms. We are now in a position to see that the answer, in time-honoured intellectual fashion, is yes and no. They were to the extent that they supplied different exemplars (Kuhn's own preferred meaning of 'paradigm'). But they were not to the extent that the theories were commensurable, with enough in common to permit efforts at making each the appendage of the other. Biometry and Mendelism confront us not with incommensurability—different theories answering to different data—but with another familiar epistemological condition, that of underdetermination—different theories answering to the same data. As such, the path is open to the counterfactualist historian to see how far Weldon's early efforts at biometrizing Mendelism can be extended.[45]

[43] 'Probably both views, the Galtonian and the Mendelian, will be reconciled in time in a wider generalisation of the facts of inheritance and descent—a larger theory of heredity', was how Weldon put it near the start of his seventh London lecture on inheritance. However, he devoted the rest of the lecture, and the final lecture too, to the problems plaguing Mendelism. [Weldon], op. cit. note 25, 732, 810, quotation on 732. In his unpublished book manuscript, Weldon expanded: 'Mendel's work and Galton's are ... in a sense complementary, the one dealing with the case in which selective mating is carried to its extreme limit among the ancestors of the stock observed, while the parents belong to distinct races, the other dealing with the stock produced by parents of a single race, in which selective mating is reduced to a minimum.' Quoted in Olby, op. cit. note 26, 316.

[44] See Robert Olby, 'William Bateson's Introduction of Mendelism to England: A Reassessment', *British Journal for the History of Science* **20** (1987), 399–420, esp. 412–5.

[45] For another reading of the controversy by Kuhnian lights, see Donald MacKenzie and Barry Barnes, 'Scientific Judgment: The Biometry-Mendelism Controversy', in *Natural Order: Historical Studies of Scientific Culture*, B. Barnes and S. Shapin (eds.) (Sage: London, 1979), 191–210, esp. 198–203. MacKenzie and Barnes also concluded that this was not an instance of paradigms clashing. For paradigms as exemplars, see Thomas S. Kuhn, *The Structure of Scientific Revolutions*, 2nd edition (Chicago: University of Chicago Press, 1970), 187–91, 198–204.

7. Conclusions

Might other histories have produced other, nongenic biologies? Here I have attempted less to answer the question than to dissolve some prejudices about taking it seriously, since 'no' looks so obvious. One issue considered is the too-quick joining of realism-to-inevitabilism and antirealism-to-contingentism. Another is the now-exploded idea that, around 1900, three men independently rediscovered a theory of inheritance propounded decades earlier by the forgotten Mendel. A third is the misguided temptation to count the abandonment of one nongenic biology in the actual past, Lysenkoism, against the prospects of other nongenic biologies in the possible past. A fourth is the forgetting of just how strong a position, conceptually and institutionally, the main competitor to Mendelism, ancestrian biometry, enjoyed before the death of its most able supporter, Raphael Weldon (and of course such deaths—so emblematic of contingency in history—have long been staple features of 'what if?' conjectures). A fifth is the suspicion that the post-1900 data on inheritance, laden with Mendelian preconceptions, cannot be used to test the potential for success in non-Mendelian alternatives.

Throughout I have emphasized questions of evidence, for biologists making sense of the world, and for historians making sense of biologists. In closing let me revisit two such questions, one resolved, one not. I noted that the issue on which the biometricians diverged most clearly from the Mendelians, of gametic purity ('the central dogma of Mendelism', as the historian Jean Gayon calls it), lent itself in principle to empirical checking.[46] To find out whether or not the gametes were pure, biologists could have gone ahead and examined the gametes, or—something much more tractable near the turn of the century—examined the self-fertilizing progeny of extracted recessives. Indeed, we can imagine a possible past in which the Mendelians won, and the biometricians lost, after years of patient, international toil vindicated the truth of the gametic purity of extracted recessives. But this is not what happened. After Weldon's death, doubts about gametic purity were not so much assuaged as abandoned.[47] Like all scientific programmes that

[46] Gayon, op. cit. note 20, 310.

[47] An exceptionally interesting and complex figure in this story is the Harvard geneticist William Castle. In the early days of Mendelism, he counted himself a Mendelian who doubted that gametes were pure. He was also uncomfortable with the mutationism then current among his fellow Mendelians. If Castle had not been rude about the ancestral law, the

acquire momentum, Mendelism grew to encompass all manner of exculpatory explanations. If some of the offspring of inbred extracted recessives displayed the dominant character, well, that showed that the parent organisms had not been true-breeding after all, or that there had been mutations, and so on. It did not show that Mendelism was false. By the 1940s, the only group that found these sorts of self-sealing manoeuvres remotely objectionable were the Lysenkoists.[48]

If evidence has constrained biologists so lightly, what hope is there for empirical rigour from the historian of the counterfactual biological past? More hope than one might think, as this paper has attempted to show.[49] But there are serious difficulties to be faced. Consider, for instance, the simple fact that most scientific theories change over time. In the course of change, parts of the theory can be modified and even, at the extreme, jettisoned. So there seems no reason in advance to bar the counterfactualist historian from allowing, say, the Weldonian biometricians that never were, or their successors, gradually to have cut away from the theory whatever was inadequate or inconsistent (as the Mendelians did for their theory). But if we permit that much, then it seems, in principle, that *any* unsuccessful theory from the past has to be regarded as a potentially successful theory.[50] What is needed is some criterion for

[48] See Levins and Lewontin, op. cit. note 13, 178–9.

[49] On methods and motives for engaging the counterfactual history of science, see Gregory Radick, 'The Scientific Pasts that Might Have Been, and Why They Matter', *New Scientist* (in press).

[50] A related worry is that every failed but potentially successful theory can be described as a variant—more and less extreme—of a successful theory. The upshot would be that, no matter what had happened in the science of heredity, there would be grounds for declaring the winning theory 'Mendelism'.

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ancestrians might well have seen him as one of their own, though operating in a niche—selection experiments—that they regarded as marginal. Eventually Mendelian critics persuaded Castle that experimental results apparently showing gametic impurity could be explained if one postulated the existence in pure gametes of modifier genes. See Gayon, op. cit. note 20, 310-314, and, for Castle's hooded-rat experiments as a case study in scientific realism about entities, see Marga Vicedo, 'Experimentation in Early Genetics: The Implications of the Historical Character of Science for Scientific Realism', *Biology and Epistemology*, Richard Creath and Jane Maienschein (eds.) (Cambridge: Cambridge University Press, 2000), 215–43. For Castle on the ancestral law, see Pearson, op. cit. note 23 (the 'Mendelian' of Pearson's title is Castle). I am grateful to Steve French and Jon Hodge at Leeds for helpful discussion of Castle.

deciding how different two theories need to be before they count as different theories. Such a criterion would be of interest, of course, independently of its usefulness in disciplining counterfactual inquiries.

So there is distinctively philosophical work ahead. There may also be distinctively philosophical returns. I have suggested that realism goes with inevitabilism, and antirealism with contingentism, as a matter not of logic but of psychology. That association can be turned to advantage. A common predicament for scientific realists, as Peter Lipton has pointed out, is to find antirealism both hard to refute and hard to believe.[51] Anyone with remotely realist intuitions finds it well-nigh impossible to accept, for instance, that, though the world now contains goats engineered to produce milk containing spider silk, we have no warrant to believe that a spider gene for silk-making really exists, with properties much like those attributed to it in current genetic theory.[52] What these realists require is help in seeing how such achievements could have arisen in the absence of the ideas that in fact make them possible. A decent counterfactual historiography of science could be just the therapy needed, to enable either the surrendering of stubborn realist intuitions or, as it could well turn out, a surrendering to them.

[51] Peter Lipton, *Inference to the Best Explanation*, 2nd edition (London: Routledge, 2004), 206.

[52] On the transgenic silky goats, see Lawrence Osborne, 'Got Silk', *The Best American Science Writing 2003*, Oliver Sacks (ed.) (New York: HarperCollins, 2003), 186–93.