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Mendel the fraud? A social history of truth in genetics

Abstract: Two things about Gregor Mendel are common knowledge: first, that he was the "monk in the garden" whose experiments with peas in mid-nineteenth-century Moravia became the starting point for genetics; second, that, despite that exalted status, there is something fishy, maybe even fraudulent, about the data that Mendel reported. Although the notion that Mendel's numbers were, in statistical terms, too good to be true was well understood almost immediately after the famous "rediscovery" of his work in 1900, the problem became widely discussed and agonized over only from the 1960s, for reasons having as much to do with Cold War geopolitics as with traditional concerns about the objectivity of science. Appreciating the historical origins of the problem as we have inherited it can be a helpful step in shifting the discussion in more productive directions, scientific as well as historiographic.

1. Introduction

"Factcheck study shows that Mendel's statistics add up": so read the headline of a story on the John Innes Centre website in January 2020. It reported the publication of a new paper aiming to put to rest old concerns about whether Gregor Mendel's data from his experiments with garden-pea hybrids – data that went on to become foundational for the twentieth-century science of genetics – were, statistically speaking, "too good to be true." After explaining that Sir Ronald Fisher had first raised the alarm in the 1930s, the story quoted Noel Ellis, a distinguished pea geneticist based at the Centre and lead author of the new paper, on how previous efforts to exonerate Mendel, as documented in the recent volume *Ending the Mendel-Fisher Controversy* (2008), had not gone far enough, leaving "some lingering doubt about the probity of Mendel's work, which we hope this paper has finally dispelled." As Ellis and his collaborators put it in the conclusion of their paper, also quoted: "Statistical criticism of Mendel's data has been a pernicious feature of discussions of his work and has done great damage to the reputation of one of history's most insightful biological scientists. We find Mendel's 1866 paper is exemplary both in terms of its presentation and in its interpretation of numerical data."[1]

No one reading this story would have any reason to ask themselves how and why the statistical evaluation of Mendel's data came to absorb so much scientific attention. After all, by 1936, when Fisher published the results of his analysis, Mendel had been an internationally famous scientific hero for over a quarter of a century. Of course Fisher's results would be immediately controversial; of course geneticists and others would invest time and energy in examining those results and, if possible, deciding whether there was genuine cause for concern. But in fact, for decades after Fisher published, and despite his conclusions becoming well known, there was no "Mendel-Fisher controversy" – no public brouhaha over Mendel's data and what they might indicate about Mendel's truthfulness. Still more surprisingly, when Fisher published, knowledge that Mendel's data conformed improbably closely to the predictions of his theory was long familiar among cognoscenti like Fisher.

The history of interest in Mendel's data statistically considered turns out to have an intriguing structure. One ambition in what follows is to delineate that structure. Another ambition is to explain it. I will suggest that a long-running minor concern became a major problem only in the 1960s and 70s thanks to the conjunction of an anniversary, the Cold War and a new mistrustfulness towards science. I hope to suggest too how a new understanding of the specificity of the historical causes which gave rise to the "Mendel-Fisher controversy" can throw light not just on its origins but on the too easily taken-for-granted terms of the debate.

2. The data problem discovered

We begin not with Mendel or Fisher but with W. F. R. Weldon, who in 1900 was newly installed as Linacre Professor of Comparative Zoology at Oxford. Weldon first read Mendel's paper in the autumn of that year. Over the next months, in fitful reflections about the paper, he expressed doubts about the uniformity of the pea characters Mendel described, and doubts too about the wisdom of Mendel's ignoring the ancestral histories of the pea varieties used in his experimental hybridizing. In the autumn of 1901, as Weldon wrote up his thoughts on Mendel for the new statistical-biological journal that he and his collaborator, the UCL mathematician Karl Pearson, were about to launch, *Biometrika*, Weldon began looking more closely at Mendel's data, in particular the match between the numbers reported and the numbers predicted. What, exactly, were the odds of Mendel getting such a tight fit between theory and data?

To find out, Weldon checked the "probable error" of Mendel's results from his simplest, single-character crosses, using a standard formula to calculate expected deviations from the theoretically predicted values given the number of observations made. For example, in Mendel's seed-shape cross, he reported that in the offspring of the hybrid pea plants, 5,474 out of 7,324 seeds had the dominant character of roundedness. Theoretically, the predicted number was 5,493, with a probable error of ±24.995. In other words, if the experiment were re-done at the same scale, under the same conditions, umpteen times, half the results would be expected to fall somewhere between about 5,468 and 5,518, and half expected to fall outside those boundaries. In itself, Mendel's result of 5,474, i.e., six seeds above the lower boundary, was not suspiciously good. But the fact that almost all of his results, for all seven characters, in both the hybrid offspring and in *their* offspring, fell within the probable-error boundaries was, on the face of it, remarkable. At the other extreme of complexity, Weldon found the same improbable closeness when he looked at Mendel's results for his triple-character cross, here using not the probable-error formula but a new test of Pearson's, the "chi-square test."[2]

Weldon organized his findings into table form and sent them to Pearson in late November 1901. About Mendel, Weldon wrote: "He is either a black liar, or a wonderful man" – "wonderful" in the older, literal sense of "wonder-making." For the most part, Weldon was inclined to think neither that Mendel was lying nor that he was miraculously lucky, but that he had reported truthfully on what he had observed in the particular varieties he worked with, under the conditions that he observed them in:

> [I]f you take all Mendel's figures together, they are wonderfully good approximations to his hypothetically probable results. ~~Remembering his shaven crown, I can't help wondering if they are not too good?~~ I do not see that the results are so good as to be suspicious, so that I can see no alternative to the belief that Mendel's "laws" are absolutely true for his peas, and absolutely false for Laxton's, while those of Tschermak are intermediate…. But the fear of Mendel is before my eyes. Really one has never seen such perfectly devised observations, lasting over 8 years, give a result so absolutely untrustworthy. It seems to me to show an influence of conditions so great that I feel it hardly worth while to grow any thing. If only one could know whether the whole thing is not a damned lie! Segregation of hybrids into apparently pure bred offspring can't be a lie, because every one gets such a result. But the consistent dominance, and the regularity of the separate inheritances *only in the monastery garden at Brünn!* Shall I shave my crown too?[3]

Thomas Laxton was Darwin's pea expert, whose crossing work Darwin cherished for the support it seemed to provide for his pangenesis hypothesis. Weldon cherished it for a different reason: when Laxton tracked hybrid characters in peas, his results – published in 1866, the same year as Mendel's – looked nothing like Mendel's. For where Mendel's hybrids always showed just the one parental character in color and shape, Laxton's were sometimes blended, sometimes wholly like the one parent, sometimes wholly like the other, and sometimes mosaically like both. Introducing Laxton's work to Pearson, Weldon wrote: "While Mendel was making his 'laws,' Laxton, of whom Darwin speaks so often, was crossing peas and making all the main races we now eat."[4]

Erich von Tschermak has come to be remembered as the least scientifically impressive of the rediscovery trio of Tschermak, Hugo De Vries and Carl Correns. But Weldon got a lot out of Tschermak's papers, appreciating his care in not sweeping all the variability he observed in, say, 400 yellow-green hybrid seeds into the category "yellow," but instead noticing, and recording, that 40 of them showed different kinds of not-yellow.[5] And Tschermak affirmed what Weldon suspected: that the particular varieties or "races" used mattered hugely. The more closely the conditions of a cross approximated Mendelian conditions – as was sometimes the case for Correns, Tschermak, and others – the more closely the results approximated Mendelian results, especially when the categories used were the Mendelian binaries. "There is no doubt at all," Weldon wrote to Pearson, after sending the data tables, "that the only thing Mendel or anyone else who tried to repeat his work can have done is to put each pea into one of two categories, each containing *very* variable elements, but not generally overlapping."[6] As to where all that left the black-liar-or-wonderful-man question, Weldon was a little clearer in a letter a few days later: "I believe myself, after reading the others, many of whom worked at first without knowing Mendel, – that he cooked his figures, but that he is *substantially* right.*" The asterisk took Pearson to a further comment at the top of the page: "I mean, right for particular races. – That is, the amount of dominance is a function of ancestry as well as individual character: and his attempt to treat parental character as a sort of chemical unit is rot."[7]

So some pea races were minimally variable like Mendel's; and, provided one was willing to categorize every seed as either yellow-or-green or round-or-wrinkled or whatever (and otherwise to reject it as a bad seed), hybridizing those races could well lead one to think that yellowness and greenness and roundedness and wrinkledness and so on in peas were like chemical units. But other pea races were far more variable. They were less like Mendel's peas and more like humans when it came to height and, probably, just about everything else.

That, for Weldon, was the major lesson from the improbability of Mendel's data. In Weldon's paper, published early in 1902, he calculated the odds against anyone getting results as good as Mendel for his single-character crosses as 16 to 1, and the odds against such good results for the three-character cross as 20 to 1. The paper went on to provoke what turned into years of bitter controversy with Bateson and his growing number of allies.[8]

3. The data problem "rediscovered"

"It is interesting that Mendel's original results all fall within the limits of probable error; if his experiments were repeated the odds against getting such good results is about 16 to one." Thus the young Ronald Fisher, then a mathematics undergraduate at Cambridge, in a talk he gave in November 1911 on heredity. He was addressing the Cambridge University Eugenics Society, of which he was co-founder, using the occasion to set out the basics of Mendelism and then biometry as, respectively, the theory of inheritance he accepted as true and the body of mathematical techniques he recommended for putting that theory to eugenic work, the better to "effect a slow but sure improvement in the mental and physical status of the population." He brought up Weldon's finding not to sow doubt about Mendelism, let alone impugn Mendel's integrity, but to illustrate the calculational power of the probabilistic mathematics of which biometricians were masters. Weldon was not mentioned, nor the underlying problem with Mendel's data as Weldon saw it: their classification into either/or category pairs, in accord with a flawed concept of dominance as a property that some character-versions do or do not possess, independently of context. On the contrary, Fisher reassured his fellow eugenists that context-induced variability, though needing statistical methods to describe it, could for practical purposes be ignored, since "luckily in most cases it appears to be small, and still more luckily it is not inherited."[9]

What is now known as the "Mendel-Fisher controversy" traces, of course, to a paper that Fisher published a quarter of a century later, when he was Galton Professor of Eugenics at University College London.[10] By then he had become internationally famous not only for his comprehensive Mendelizing of Darwinian biometry but for his innovations in statistical methods, especially in agricultural research.[11] Bringing to bear that side of his expertise, Fisher presented a bravura reconstruction of Mendel's program of experimental work year by year.[12] Re-analyzing Mendel's data statistically, Fisher found, like Weldon (again not cited), that they are improbably good. Indeed, Fisher went beyond Weldon in claiming to show that Mendel's data are improbably good even when, by Fisher's lights, Mendel was in error about what his theory ought to predict. In other words, whether or not Mendel identified the right prediction, his data fell into line.[13] But what that showed, Fisher now argued, was what a great thinker Mendel was. For relatively soon after the crossing experiments were underway, Mendel must have worked out his theory in the abstract; and from that moment, he knew how his data ought to look. His program of experiments thus became, in Fisher's words, "a carefully planned demonstration of his conclusions."[14] For Fisher, the data's limitations were thus largely to Mendel's credit, and such blame as Fisher was willing to consider he meted out to a well-meaning but misguided underling who, Fisher surmised, must have quietly gotten rid of whatever plants threatened to mess up the master's ratios: "Mendel was deceived by some assistant who knew too well what was expected."[15]

Again like Weldon, Fisher expressed himself more pungently in private correspondence. He wrote to the Oxford population geneticist E. B. Ford in early January 1936: "I have had the shocking experience lately of coming to the conclusion that the data given in Mendel's paper must be practically all faked." Calling this an "abominable discovery," Fisher nevertheless affirmed his faith in Mendel's honesty: "I don't believe that this touches Mendel's own *bona-fides* or the reality of the experiments he carried out."[16]

Indeed, in the paper, Fisher styled himself as the *defender* of Mendel's good name, against the sullying imprecations of – of all people – Bateson.[17] A few days later, in a letter to the Innes-based cytologist Cyril Darlington, Fisher suggested that it may well have been Mendel's uncompromising assiduity in the empirical testing of his theory that provoked his assistant into some labor-saving fabrication: "In one case, an experiment giving widish deviation was repeated, at the expense of growing 1000 additional plants, and this may have convinced his assistant that Brother Gregory had better not be grieved again by unexpected discrepancies."[18] Writing the next day to the journal editor who had solicited the paper, Fisher wrote: "I had not expected to find the strong evidence which has appeared that the data had been cooked. This makes my paper far more sensational than ever I had intended, and adds another mystery to those that have been puzzling me, some of which I think I had made some progress with."[19]

In keeping with Fisher's intentions, however, over the decades that followed, his demonstration of the improbably close match between Mendel's expected and observed results became familiar, in and out of genetics, not as a shameful instance of scientific fraud but as an illustration of how to run a chi-square test and why doing so is important.[20] Whatever disquiet geneticists may have felt in making sense of Fisher's analysis they kept to themselves.

4. 1948 and all that

From 1948, the arrival of anti-Mendelian, pro-Lamarckian Lysenkoism on the world stage turned public silence into a political imperative. There was no mention at all of the too-good-to-be-true data problem in Julian Huxley's *Soviet Genetics and World Science* or

Conway Zirkle's *Death of a Science in Russia*, two 1949 books notable for their boosterism about the power of Mendelian breeding in agriculture. (Discussing Mendel's discovery of the 3:1 ratio of dominant to recessive character-versions in the offspring of his hybrids, Huxley aggregated Mendel's data on seed color with the data of seven later investigators, then invited readers to marvel at how, with over two hundred thousand seeds in the trans-historic sample, the ratio comes out as 3.003 to 1.)[21] Accentuating the positive became official policy for the Genetics Society of America, which used its 1950 conference on the "Golden Jubilee" of the triple rediscovery to celebrate Mendel and his legacies, above all in agriculture, with the whole of the upbeat proceedings recorded for broadcast beyond the Iron Curtain by the propagandizing Voice of America. Again, there was no hint of a problem with Mendel's data.[22]

When Zirkle, a speaker at the conference, published a short piece in *Science* four years later on "Citation of Fraudulent Data," he dealt exclusively with the Lysenkoists and their British fellow travellers. Especially exasperating to Zirkle was the latter's fondness for citing the work of Paul Kammerer, an Austrian physiologist who had become notorious in the 1920s for supposedly demonstrating Lamarckian inheritance of acquired characters in breeding experiments with midwife toads, and whose suicide was widely interpreted as an admission of the fraud he was accused of by Bateson and others. Nor was Zirkle convinced by attempts at exculpation of Kammerer along exactly the lines that Fisher in the 1930s pursued on Mendel's behalf:

> Western biologists as a whole have tended to excuse Kammerer and blame the fakery on some overzealous assistant. Such "assistance" was actually given the great Russian physiologist I. P. Pavlov. At the International Congress of Physiology held in Edinburgh in 1923, Pavlov announced that he had proved that the conditioning of

> reflexes was inherited. This turned out to be false, and Pavlov retracted the statement…. Although it is remotely possible that Kammerer, like Pavlov, was fooled by an assistant, the probabilities are against such an interpretation.[23]

Zirkle – a botanist-turned-historian, based at the University of Pennsylvania – remained in full Cold Warrior mode through the rest of the decade. The most overtly political contribution to the 1959 *Origin* centennial was his *Evolution, Marxian Biology, and the Social Scene* (1959), a lengthy treatise combining a history of the rise of Malthusian Darwinism, Mendelian genetics, Galtonian eugenics, and their synthesis with a history of the emergence of the Marxian negation of all that, together with a study of Marxian influence among humanities scholars and social scientists in the United States. Again, fraud comes across as exclusively, and endemically, Lamarckian.[24]

Within the philosophy of science, meanwhile, the mid-century shift away from inductivism proved a good fit with Fisher's reading of the Mendel case. In a 1948 paper that Zirkle cited approvingly, the London theoretical biologist and philosopher of biology J. H. Woodger invoked Mendel's example in urging embryologists to be bolder in standing back from their data and framing the sort of explanatory hypotheses that, history showed, were the key to transformative scientific advance:

> The heaping up of data may retard rather than facilitate the coming of the desired explanatory hypothesis, by diffusing and distracting attention over too wide a field in the first instance. What is wanted is a great concentration of attention on a few suggestive statements. Mendel can have had but scanty data to reflect upon. But his hypothesis could have been reached simply by reflecting upon the 50:50 sex ratio in conjunction with certain very general scientific principles. It may be that Mendel did

> reach his hypothesis in some such way as this and devised his garden experiments as a means of testing it.[25]

Even so, among themselves, far from the public stage, a number of geneticists continued to generate explanatory hypotheses about Mendel's too-good data. George Beadle and Alfred Sturtevant had a go, looking at whether quirks in the pollen-production mechanism in peas might be responsible, but concluded that, although this possibility would account for the direction of the bias in Mendel's results, it would not account for the magnitude.[26] When Curt Stern, on a visit to Madison in early 1955, heard that the not-yet-arrived Sewall Wright had interesting things to say on the topic, Stern wrote to Wright, receiving in reply a fascinating letter where Wright gave his reasons for thinking that unconscious bias, rather than deliberate falsification, had been in play.[27] The Czechoslovak biologist-turned-historian Vítězslav Orel recalled that the Mendel data question had been much discussed between him and his own mentor in Mendelian genetics, Jaroslav Kříženecký. In the latter's view, it was down not to pea reproductive physiology, unconscious bias, or outright fraud, but to Mendel's no longer bothering with the scoring of peas once his expected ratios were confirmed – a practice followed in innocence of what later statistical theory would counsel.[28]

5. Open minds in the free world

The year of *Evolution, Marxian Biology, and the Social Scene* was also the year that Nikita Khrushchev let himself be photographed amidst that emblem of Mendelian bounty, an Iowa cornfield. As de-Stalinization loosened Lysenkoism's grip in the Soviet sphere, the sense of emergency among geneticists outside that sphere subsided. Soon the geneticists began to participate in a wider trend within Western, and especially American, culture in that phase of the Cold War: the celebration of the human mind in a state of freedom to think and create without limits. From government departments and think tanks through to the cognitive science laboratories being set up at prestigious universities, there was a growing emphasis on exploring and, crucially, promoting the "open mind" as what defined humans at their rational and democratic best. An open mind was one not captive to dogmatic certitudes but free to probe even cherished beliefs as potentially mistaken. Habits of criticism, including self-criticism, were held up as vital, along with the freedom to speak and write honestly about one's conclusions. Freedom meant the freedom to think about anything, to question anything, to be transparent about flaws and difficulties. For those eager to inhabit or, for propagandistic purposes, exhibit the distinctive strengths of what was known as "the free world," self-critical science was thus of a piece with civil-rights marches and abstract expressionism.[29]

Right in step, at the next Mendel anniversary in 1965–6, silence over the Mendel data problem gave way to volubility. An early entrant in the new conversation was Zirkle, in a 1963 lecture (published the next year) on "the delayed discovery of Mendelism":

> Some modern statisticians, who are armed with the mathematical tools of modern statistics, have reported that Mendel's results were significant – in fact, a little too significant. They were a little too good, better than we would have a right to expect purely on the basis of chance. Could the good Father Mendel have fudged his results just a little? Could he have omitted a few unusual ratios? It could be, but here we shall have to introduce an uncertainty factor. If Mendel's ratios had not been excellent – perhaps by chance – he might never have discovered Mendelism.

Zirkle then underscored the fragility of that discovery – its dependence on the counted plants organizing themselves cleanly into exact, explicable ratios – by doubling down on his counterfactual, wondering, conversely, whether Darwin might have discovered Mendelism had his ratios, when he crossbred hybrids unto the second generation, been just that little bit closer to 3:1.[30]

Other public commentators over the anniversary period included Beadle, Sturtevant, L. C. Dunn, Wright and Theodosius Dobzhansky, and two British biologists, the embryologist Gavin de Beer and the marine biologist Sir Alister Hardy.[31] None thought that an accusation of fraud was justified; all thought there was nevertheless something to be explained or, preferably, explained away. "A variety of explanations to exonerate Mendel from this monstrous accusation have been suggested by Fisher himself and by the authors mentioned above," wrote Dobzhansky, in an omnibus 1967 review of the centennial Mendeliana in *Science*. He went on to give his own exonerating explanation: that Mendel, in common with skilled experimentalists before and after him, had probably thrown out data that he judged aberrant – perhaps due to plants becoming contaminated with foreign pollen.[32]

The sense of a taboo being broken is palpable in contemporary correspondence between Wright and Stern. Wright's article, "Mendel's Ratios," was published at Stern's invitation in a volume of Mendel source materials that, as Stern had explained to Wright in an October 1965 letter, was planned to include Fisher's 1936 paper. Wrote Stern:

> The objection has been voiced that to have Fisher's paper in this volume might incline the reader to become skeptical about Mendel's contributions, which, after all, are the inspirations of our volume. It occurred to me that it would be most valuable to append to Fisher's paper the content of your letter… I am sending you herewith a

> copy of that letter and would be very grateful to you if you give us permission to make use of it. Possibly you may want either to add or change some items.[33]

Wright had, in fact, forgotten about his earlier letter to Stern, and had recently written up much the same thing for Dunn, in relation to Dunn's anniversary book. A version of the new piece was what Stern eventually published.[34]

6. Mendel comes in from the cold

As to why this inconclusive discussion inaugurated a minor but steadily active – indeed ongoing – academic industry, we need to turn to Cold War culture on the other side of the Iron Curtain. Among the anniversary meetings was one in Mendel's hometown, the former Brünn, now Brno. Yes, Khrushchev in Iowa in 1959 had signalled to the world the beginning of the end of Lysenkoism.[35] Even so, when Lysenko visited Prague the next year, he was received as an honored guest. Around that time Mendel's statue in Brno was removed from public view.[36] Lysenkoist deprecations of him aside, Mendel – as a Catholic prelate in a fabulously wealthy monastery, and a cultural German beloved of the Nazis, whose brutal occupation of Czechoslovakia was still a fresh memory, and who had planned to set up a Mendel Research Institute in Brno to advance genetics "in the spirit of German National Socialism" – was not at all an easy figure for Czechoslovak Communist officialdom to celebrate.[37] So the politics were delicate when, in 1963, the Academy of Sciences nevertheless got behind the project to hold an international, UNESCO-funded Mendel symposium. The man who eventually made it happen, Vítězslav Orel, a former poultry researcher turned historian of science, understood his brief, and used his symposium address to stress Mendel's credentials as someone who, befitting a socialist hero of science, belonged to the world of practical agricultural and horticultural improvement.[38] If ever there was a time *not* to mention the data problem, the Brno meeting was it. And no one did mention it, not even Zirkle, who courteously left it out of a rerun of his delayed-discovery lecture.[39]

Only a few years later, when the Czechoslovak rehabilitation of Mendel was well in hand, taking institutional form in a new Mendel museum in Brno and a new research journal (both run by Orel), did Orel face down that less-than-heroic theme of the centennial. Unsurprisingly, Orel's view was that much ado had been made of nothing, and in relation to someone whose meticulous recordkeeping, as preserved in the documents preserved in the Brno collection, was beyond reproach. Yet Orel's "Will the Story on 'Too Good' Results of Mendel's Data Continue?" backfired completely. Far from killing the story dead, Orel gave it permanent vigor, partly by publicizing it for readers who would never have bothered reading the anniversary papers and volumes *en masse*, and partly by summarizing so ably the abundance of surmises already in play: about what Mendel had or had not done as well as about which statistical tests to apply, how to apply them, and how to interpret the results.[40]

So forbiddingly technical were the issues raised that the "Mendel-Fisher controversy" might well have remained a matter strictly for specialists. But word began to spread. In the pro-Kammerer bestseller *The Case of the Midwife Toad* (1971), Arthur Koestler turned the tables on the likes of Zirkle, suggesting that it was not the Lamarckians but the Mendelians who had the foundational fraud problem. "It is rare," wrote Koestler, after introducing Fisher's analysis, "to find this historical scandal mentioned in the literature. It was not so much hushed up as shrugged off. Since Mendel's Laws had been shown to be correct, what does it matter if he cheated a little?" Quoting at length from Hardy, who had speculated in Fisherian fashion about well-meaning assistants, Koestler added: "Tolerance and broadmindedness towards the dead are no doubt laudable; but what if that obscure monk in

Brünn had been caught red-handed doctoring his statistics – or even neglecting to check the gardeners' statements?"[41]

The following year a horticultural journal played it all for laughs:

PEAS ON EARTH

In the beginning there was Mendel, thinking his lonely thoughts alone. And he said: *"Let there be peas,"* and there were peas and it was good.

And he put the peas in the garden saying unto them *"Increase and multiply, segregate and assort yourselves independently,"* and they did and it was good.

And now it came to pass that when Mendel gathered up his peas, he divided them into round and wrinkled, and called the round dominant and the wrinkled recessive, and it was good.

But now Mendel saw that there were 450 round peas and 102 wrinkled ones; this was not good. For the law stateth that there should be only 3 round for every wrinkled.

And Mendel said unto himself *"Gott in Himmel, an enemy has done this, he has sown bad peas in my garden under the cover of night."*

And Mendel smote the table in righteous wrath, saying *"Depart from me, you cursed and evil peas, into the outer darkness where thou shalt be devoured by the rats and the mice"* and lo it was done and there remained 300 round peas and 100 wrinkled peas, and it was good. It was very, very good.

And Mendel published.[42]

8. The data problem meets the new public mistrustfulness

What transformed this minor theme of modern Mendeliana into a major one was the congruence with a larger image problem which overtook Western science in the 1970s. Somewhere between, let us say, Rachel Carson's revelations about the chemical industry's poisoning of the environment, the ceaseless images of technoscience-delivered devastation of the people and landscapes of Vietnam, and the struggle for justice for children born deformed because their mothers had taken the pregnancy drug thalidomide (to cite just three of the best-remembered lows), the moral high ground taken for granted in the polemics of the Cold War at its frostiest was lost.[43] Along with that détente-accelerated shift came an enlarged public appetite for learning about cases of scientific fraud, such as the revelations about the British psychologist Sir Cyril Burt, whose twin studies purporting to show that intelligence is genetically determined had been exposed as fake.[44] In a 1977 review essay on the IQ controversy in the *New York Review of Books*, the British immunologist Sir Peter Medawar brought up the Mendel case in exploring – and then exploding – a possible line of defense for Burt (along the way summarizing, with trademark crispness, the Lysenkoist take on Mendel):

> There is, as a matter of fact, a well-established precedent for the selection or adjustment of figures to fit a preconceived hypothesis: R. A. Fisher, at that time the world's foremost authority on small-sample statistics, once pointed out that Mendel's famous segregation ratios (3:1, 9:3:3:1) were numerically much too good to be true. Given the size of his samples, no such degree of conformity to theoretical anticipation could be judged plausible. Whatever R. A. Fisher's motives may have been in calling attention to this fact, we may be quite sure it was not his intention to show Mendel up as a running-dog of Fascism (as the faithful later came to call him). The most

plausible explanation seems to be that the abbé's gardeners and assistants had formed a pretty clear idea of what ratio Mendel was expecting, and whether out of loyalty or affection supplied their reverend employer with results they thought he would like to hear.

There is, however, a profoundly important difference between the cases of Mendel and of Burt: Mendel was right.[45]

Mendel and more recent scientific fraudsters were likewise linked in a mood-capturing, higher-profile piece later that year in *Esquire* magazine, "Great Fakes of Science," by the American science and mathematics popularizer Martin Gardner. "Politicians, real-estate agents, used-car salesmen, and advertising copy-writers are expected to stretch facts in self-serving directions," Gardner wrote, "but scientists who falsify their results are regarded by their peers as committing an inexcusable crime." Alas, he continued, "the sad fact is that the history of science swarms with cases of outright fakery and instances of scientists who unconsciously distorted their work by seeing it through lenses of passionately held belief." High up on Gardner's list: Mendel – "such a hero of modern science that scientists in the thirties were shocked to learn that this pious monk probably doctored his data…. They are too good to be true."[46]

Somewhat to my surprise, I have not found evidence of the too-good-to-be-true data problem being used against Mendel in the Communist East until *after* the problem had attained its belated wider currency in the West. A 1984 article in *Science News* began with an anecdote from China:

> A U.S. geneticist recently touring China was approached by a local student. The student asked whether the geneticist had heard of a British statistician named Fisher

> and of a paper demonstrating that Mendel's experimental results were too good to be true. The geneticist replied, yes, the paper was well-known. The student inquired, then why hadn't Mendel's name been expunged from the textbooks and historical references to his work erased?[47]

With Mendel now world-famous as a fraudster, it is no surprise that in a book on the fraud problem in science published in 1985, he took his place in a concluding chronology of scientific frauds. (He was in excellent company: before him were Hipparchus, Ptolemy, Galileo, Newton, and Dalton.)[48] And there Mendel remains. He may be the father of genetics, but he is also "the father of scientific misconduct."[49]

9. Conclusion

Since the 1960s and 70s, when, as we have seen, the "Mendel-Fisher controversy" came into being, first as an anxious theme in the centennial reflections of professional geneticists, then as part of a broader indictment of untrustworthy science, the controversy has rumbled on and on, for the most part to little effect.[50] Title promise notwithstanding, what *Ending the Mendel–Fisher Controversy* offered was not a resolution so much as a plea for, in Koestler's phrase, shrugging off the difficulties, as both irresolvable and unfairly hurting Mendel's reputation.[51] The consensus view is more or less where it was at the start: Mendel's data are indeed improbably good, but that in itself is not evidence of fraud, nor is there any other evidence to suggest fraud. As Fisher said in 1911: "It may have been just luck; or it may be that the worthy German abbot, in his ignorance of probable error, unconsciously placed doubtful plants on the side which favoured his hypothesis."[52]

Luck or unconscious bias (or worse): that framing, set by the eugenical Fisher and solidified by the peculiar geopolitics of the Cold War, has ensured an ultimately sterile debate. What has been consistently overlooked is the possibility that, as Weldon thought, Mendel's too-good-to-be-true data show the shortcomings of working with only two categories. Assume that pea seeds must be either "yellow" or "green", "round" or "wrinkled," and you will indeed be at risk of assigning seeds that are, in Fisher's terminology, "doubtful," to whatever category will vindicate your prediction. You can try to figure out a way of deciding which of the two categories each pea *really* goes in. Or – with Weldon – you can instead give up on the categorizing and take the variability you actually see as what it is you are trying to explain: variability brought about because genes have the effects that they do in complex contexts.[53] A better understanding of how the Mendel-Fisher controversy came about can help biologists, and their students, move beyond not just the debate but beyond the determinist conception of genetics it presupposes.[54]

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[1] Anon. 2020; Ellis et al. 2019, discussing Franklin et al. 2008 and Mendel 1866.

[2] Weldon 1902, 232–5. For Weldon's probable-error formula, see 233 (cf. Davenport 1899, 14; Harris 1912, 741–2). For Pearson's now-famous test, see Pearson 1900. The mathematical challenge of applying it was made much simpler by tables that an actuary, W.

Palin Elderton, included in a paper (Elderton 1902) submitted to *Biometrika* in mid-October 1901 and published in the same issue as Weldon's on peas. Weldon had earlier confessed that he had struggled to follow Pearson's original paper, so much so that Pearson should feel free to ask for his copy back if he was running short: Weldon to Pearson, 8 Oct. 1900, Pearson/11/1/22/40, Papers of Karl Pearson (PP), Special Collections, University College London.

[3] Weldon to Pearson, [undated but, on internal evidence, between 21 and 25 Nov. 1901], Pearson/11/1/22/40, PP, crossing-out and underscoring in original. Parts are quoted in Magnello 2004, 23.

[4] Weldon to Pearson, 21 Nov. 1901, Pearson/11/1/22/40, PP; Laxton 1866.

[5] Weldon 1902, 238; Weldon to Pearson, 28 Nov. 1901, Pearson/11/1/22/40, PP. Three letters from Weldon to Tschermak, 1901–2, are preserved in the Tschermak Papers, Box 4, Folder 84, Archive of the Austrian Academy of Sciences, Vienna. Many thanks to Sander Gliboff for alerting me to them and sharing his transcripts. In a letter of 21 Nov. 1901, Weldon replied to Tschermak: "I am especially interested to find that you now think Mendel's laws only special cases of something much wider and more general.… I had felt bound to form this conclusion myself, as the only way of reconciling the published statements; but it is very difficult for one who is not familiar with the phenomena described to trust his judgment of the evidence; so that I was very glad to read your statement of your latest work."

[6] Weldon to Pearson, 25 Nov. 1901, Pearson/11/1/22/40, PP, emphasis in original.

[7] Weldon to Pearson, 28 (?) Nov. 1901, Pearson/11/1/22/40, PP, emphasis in original. (The question mark in the date is Weldon's.)

[8] Weldon 1902, 232–5. On the Weldon–Bateson debate and its significance, see Radick, in press.

[9] Fisher 1911, quotations on 160, 161 & 156 respectively. For discussion see MacKenzie 1981a, ch. 8, esp. 189–90 and Mazumdar 1992, 96–102.

[10] The indispensable guide for study of the controversy is Franklin et al. 2008. The cultural history I offer here is my interpretation of the chronology and bibliography set out in this superb volume, notably in ringmaster Allan Franklin's lengthy introduction, Franklin 2008.

[11] The capstone books from these years are Fisher 1925, 1930 and 1935. On Fisher's campaign, in Donald MacKenzie's phrase, to "*use* Mendelism to vindicate biometric eugenics," see Norton 1978, esp. 486–9; MacKenzie 1981a, 188–93, quotation on 189, emphasis in original; and Mazumdar 1992, 107–10. On Fisher's period as statistician at the Rothamsted Experimental Station from 1919 to 1933, see Parolini 2015 and Hall 2007.

[12] Published in the new history-of-science journal *Annals of Science* in spring 1936, Fisher's reconstruction appears to be an instance of "teaching-led research": the earliest signs of it are in lectures that Fisher gave at UCL in the autumn of the previous year on the history of biometry. See Stigler 2008; also Edwards 1993, 134–5, though Edwards identifies the lectures as taking place in the winter at Rothamsted. I am grateful to Stephen Stigler for alerting me to the existence of these lectures and also for sharing his knowledge and sources with me.

[13] See Fisher 1936, 125–6, 128–9, 132; for discussion see, e.g., Stigler 2008.

[14] Fisher 1936, 122–4, quotation on 124. In reaching this view of Mendel, Fisher declared a quasi-prediction of his own, published in *The Genetical Theory of Natural Selection* (1930), vindicated: that, from the mid-nineteenth century, a sufficiently bold thinker could have inferred the Mendelian nature of inheritance from a small number of then-reasonable presuppositions. "I had at that time no suspicion," wrote Fisher, "that Mendel had arrived at his discovery in this way" (123). See Fisher 1958, 7–9.

[15] Fisher 1936, 132.

[16] Fisher to Ford, 2 Jan. 1936, in Bennett 1983, 199–200, with further discussion in a letter of 15 Jan. (200–1).

[17] Fisher 1936, 116–20. Bateson, of course, revered Mendel, and would never have suggested that the experiments that Mendel wrote about in his 1866 paper were fictional. Fisher spun the accusation out of a minor footnote added by Bateson to the English translation of Mendel's paper. Commenting on Mendel's description of the varietal pairs used in each of his initial crosses as differing only "in one essential character," Bateson advised that, given the practical difficulties involved in fulfilling that description literally, readers should suppose that Mendel meant that, in whatever ways the members of his pairs differed, they were irrelevant to tracking the character of interest: seed color, or seed shape, or whatever. On that slender basis Fisher represented Bateson as having cast doubt on whether anything Mendel wrote about his experiments was to be taken literally.

[18] Fisher to Darlington, 7 Jan. 1936, Folder J.47, Ms.Darlington.c.107, Papers of C. D. Darlington, University of Oxford. Many thanks to Alex Aylward for sharing this letter with me.

[19] Fisher to Douglas McKie, 8 Jan. 1936, quoted in Bennett 1965, vii.

[20] Gigerenzer et al. 1989, 149–52. From Fisher's work, the use of Mendelian examples to illustrate the statistical testing of hypotheses spread to such an extent that "[m]any pure statisticians and non-biological experimentalists came to know at least the rudiments of Mendelian genetics through these illustrations" (151). For an earlier attempt, explicitly indebted to Weldon, to promote such tests among Mendelians, see Harris 1912 (which aimed at improving the Weldon-inspired discussion in Johannsen 1909, 402–10).

[21] Huxley 1949, 108. Cf. the tart remarks on the closeness of Mendel's observed and predicted values for yellow and green pea seeds in the Lamarckian E. W. MacBride's 1924 *An Introduction to the Study of Heredity* ("The student will do well to regard with the utmost

suspicion figures adduced to prove the proportions of strains appearing in the progeny of hybrids if these figures indicate comparatively small numbers.") MacBride 1924, 147; discussed in Bowler 1983, 101.

[22] On the 1950 conference – which included an extraordinary "New World Honors Mendel" ceremony, saluting the role of Mendelian breeding in American and, increasingly (via hybrid corn), Latin American agriculture – see Wolfe 2012. Whether the recording was broadcast is not known, but the proceedings were published in Dunn 1951.

[23] Zirkle 1954, quotation on 189. I have omitted a couple of references.

[24] Zirkle 1959. On Zirkle as Cold Warrior see DeJong-Lambert 2012, 153–8.

[25] Woodger 1948, 356; Zirkle 1951, 100.

[26] Recalled by Beadle in Beadle 1967, 337. He did not give a date, saying only that the collaborative work had taken place "some years ago."

[27] Wright to Stern, 25 Feb. 1955, in Folder 2, MS COLL. No.5, Papers of Curt Stern, American Philosophical Society, Philadelphia.

[28] Orel 1968, 777.

[29] On these emphases in the culture of Cold War science in the West see esp. Cohen-Cole 2014 and Rasmussen 2014, ch. 1. On that culture generally see Wolfe 2019. An exception that proves the rule is Thomas Kuhn, whose picture of scientific progress as dependent on closed minds seriously alarmed some Cold Warriors in his circles; see Riesch 2016.

[30] Zirkle 1964, quotation on 66. Zirkle cited Darwin's results not with snapdragon flowers (the standard example of Darwin's Mendelian near-miss) but with corn grains.

[31] Beadle 1967, 336–9; Sturtevant 1965, 12–16; Dunn 1965, 12–13; Wright 1966; Dobzhansky 1967; De Beer 1964, 199–203; Hardy 1965, 89. For discussion of most of these, and other commentators too, see Franklin 2008, 29–39.

[32] Dobzhansky 1967, quotation on 1588.

[33] Stern to Wright, 25 Oct. 1965, in Folder: "Stern, Curt, 1932-1967," MS Coll. No. 60, Series I, Papers of Sewall Wright, American Philosophical Society, Philadelphia.

[34] Wright to Stern, 9 Nov. 1965, in in Folder: "Stern, Curt, 1932-1967," MS Coll. No. 60, Series I, Wright Papers.

[35] Khrushchev's criticisms of Lysenko in the USSR began in 1957. Tragically, Kříženecký, misjudged the situation and right away published his own critique, leading to his arrest and imprisonment. See Orel 1992, esp. 491.

[36] In June 1959 Lysenko was elected to the Czechoslovak Academy of Sciences, whose general assembly in Prague he addressed the following April; Šimůnek & Hossfeld 2013, esp. 87. On the removal of Mendel's statue as ordered in 1959 or 1960, see, respectively, Orel 1996, 315 and Paleček 2014, 2. (The statue seems to have been moved twice: first, in 1950, after the monasteries were closed, from its prominent position in Mendel Square to the Basilica next to the Abbey; then, around 1960, from the Basilica to the yard inside the Abbey. Many thanks to Pavel Paleček and Ondřej Dostál for discussion.)

[37] On Mendel's awkwardness for "an atheistic totalitarian regime that was fighting the bourgeoisie and clericalism," see Paleček 2016, 4–5, quotation on 5; also Orel 1992, 492. On the Brno institute, see Paleček 2014, 1–2, quotation on 1, and more extensively Paleček 2004. It cannot be overestimated how high anti-German feeling ran after the war, how fully Mendelism was tarred with the brush of "fascist pseudo-science" (Šimůnek & Hossfeld 2013, 85), and how sincerely some Czechoslovak biologists wished to be a part of building a socialist alternative. For an overview of Lysenkoism in Czechoslovakia see Matalová & Sekerák 2004.

[38] Orel 1966. The role of symposium organizer fell to Orel only after the death of Kříženecký, who was asked to take it on after the death of the initiator, the Prague geneticist K. Hrubý. See Orel 1992, 492. On Orel's life and work, see Paleček 2016.

[39] Zirkle 1966. The Berkeley geneticist I. Michael Lerner, in a lecture on Mendelism and animal breeding, quoted from Fisher's 1936 paper, but only his closing reflections about how each generation since Mendel had read the preoccupations of its own time into Mendel's paper. Lerner 1966, p. 196, quoting from Fisher 1936, 137.

[40] Orel 1968. Orel laid great store by recent exonerating work published in German which, again, might well have escaped Anglophone notice, notably by the Bonn-based Franz Weiling, who spent the rest of his long career defending Mendel's reputation. On Orel's own career-long concern to protect that reputation, whatever his own research turned up, see Paleček 2016, 9.

[41] Koestler 1971, 47–8. On the popular success of the book see Buklijas and Taschwer 2019.

[42] Doyle 1972, emphases in original; quoted in Broad & Wade 1985, 235, note 24.

[43] On this period in the cultural life of science see, e.g., Agar 2012, ch. 17. On molecular biology as riding the up-and-down fortunes of Cold War science funding, see Rasmussen 2014, discussed in Radick 2016b.

[44] Martin Gardner provided a handy list of mid-1970s scandals: in 1974, over the New York cancer researcher William Summerlin's faked skin-graft results and over the North Carolina parapsychologist J. B. Rhine's faked psychic-egg results; in 1975, over the British parapsychologist Samuel Soal's faked ESP results (long circulating but given new publicity in the wake of his death that year, when the threat of libel lawsuits evaporated); in 1976, over Burt's data. See Gardner 1981, 126–9.

[45] Medawar 1977, 181.

[46] Gardner 1977, though I quote from Gardner 1981, as the 1977 version was rather heavily (and somewhat improvingly) edited. In the 1981 version, Gardner cites Koestler 1971, and shows every sign of having learned about Fisher's 1936 paper initially from Koestler.

[47] Miller 1984, discussing Root-Bernstein 1983.

[48] Broad & Wade 1985, 227.

[49] Quotation from Montgomerie & Birkhead 2005, 17. I first took up an interest in the history reconstructed here because, after every public talk I gave on Weldon and peas, someone asked about the data problem (though I had not mentioned it).

[50] In his 2004 book on scientific fraud, the historian of science Horace Freeland Judson observed both the "mounting ingenuity" expended on Mendel's behalf and the exiguous results ("The hopeful defenders, often distinguished geneticists, make up a roster of frustration and bafflement"); Judson 2004, 52–8, quotations on 56.

[51] Franklin et al. 2008; Stigler 2008. When *Ending* came out, Franklin had already spent decades defending the rational credentials of experimental physics against social-constructionist nay-saying.

[52] Fisher 1911, 160. In contrast, further research into Kammerer's case has led, in the words of one of my reviewers, "to his removal … from the annals of scientific fraud." See esp. Taschwer 2016.

[53] Overlooked is not, however, the same as omitted. Wright, in his 1955 letter to Stern, cited the work of Weldon's student A. D. Darbishire as showing that, in the garden pea, "[s]ome of the characters (especially the seed characters) give enough intermediates … to allow a good deal of leeway and unconscious bias by one not thoroughly aware of the dangers." There have, to my knowledge, been two subsequent rediscoveries of Weldon's diagnosis of Mendel's data problem: Root-Bernstein 1983 and Weeden 2016. The former shows no sign of knowing Weldon's views, and the latter mentions them only because I brought Weldon's work to the author's attention, after I heard him present a talk on his analysis at a Mendel sesquicentennial meeting, held at St. Thomas' monastery in Brno in September 2015. During the coffee break afterward I had the privilege of listening in as Professor Weeden and another pea geneticist disagreed with each over whether *Pisum sativum* presents, in Weeden's phrase,

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"ambiguous phenotypes." In Weeden's experience, they were a commonplace. For his interlocutor, they never happen.

[54] See Radick 2015.