Whatever Happened to Reversion?

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Abstract

The idea of 'reversion' or 'atavism' has a peculiar history. For many authors in the late-nineteenth and early-twentieth centuries – including Darwin, Galton, Pearson, Weismann, and Spencer, among others – reversion was one of the central phenomena which a theory of heredity ought to explain. By only a few decades later, however, Fisher and others could look back upon reversion as a historical curiosity, a non-problem, or even an impediment to clear theorizing. I explore various reasons that reversion might have appeared to be a central problem for this first group of figures, focusing on their commitment to a variety of conceptual features of evolutionary theory; discuss why reversion might have then ceased to be an interesting phenomenon; and, finally, close with some more general thoughts about the death of scientific problems.

Keywords: reversion, atavism, Charles Darwin, Francis Galton, Karl Pearson, W.F.R. Weldon, R.A. Fisher

It is a striking fact that many of the earliest presentations of evolutionary theory seem, by and large, recognizable from a contemporary perspective. As a result, our attention may be drawn all the more to those cases where significant gaps appear between the understanding of evolution offered by authors like Darwin, Bateson, or Fisher, and our own. Much ink has been spilled, for example, on the role of Darwin's principle of divergence, which rapidly moved from being a crucial part of his argument in the *Origin* to disappearing entirely from evolutionary thought (e.g., Mayr, 1992; Kohn, 2009).

Another such case is the phenomenon of "reversion" or "atavism" (and its myriad synonyms: "regression," "retrogression," "return," and so forth) with its intimate connection to the loaded, nineteenth-century sense of "ancestry." Beginning with the pigeon-breeding of Darwin, and continuing through the development of early quantitative approaches to heredity crafted by authors like Francis Galton, W.F.R. Weldon, and Karl Pearson, there was widespread emphasis on the surprising nature and supposedly extensive empirical observation of cases in which organisms were born with traits that had not been expressed in their lineage for many generations. Darwin's pigeons, for instance, despite having been bred for quite some time to exhibit peculiar, highly derived

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forms, could, he argued, revert to the appearance of their distant, wild-type ancestors after just a few crosses. Reversion quickly became one of the features of inheritance that any future theory, it was thought, would necessarily have to describe.

On the other hand, just a few decades later, R.A. Fisher would refer to reversion only in a historical context, as a problem for Darwin which never quite fit within the frame of his theory of pangenesis. By the late 1930s, we would see public calls for its removal from the biologist's lexicon.

In this paper, I want to explore the rapid rise and equally rapid fall of reversion. First, I will consider what about empirical observations of reversion might have been so surprising to and important for thinkers like Darwin, Weismann, Galton, and the biometrical school, among others. I'll then turn to those who were more conflicted about, and eventually rejected, reversion as a "problem" for biological study. In particular, I will argue here for an emphasis on the fact that authors like Darwin, Galton, Pearson, and Weldon were deeply committed to certain kinds of conceptual features that they believed any understanding of evolutionary theory would need to exemplify (such as gradualism, statistical theorizing, or population-level analysis). These features, as I hope to show, could have rendered the phenomena of reversion particularly salient – or, when interpreted somewhat differently, could lead an author like Fisher to cast it aside as irrelevant.

This stands in marked contrast to several other possible explanations for the disappearance of reversion which I will also discuss, including changes in the target audiences for these authors' work (e.g., the increased interaction between biologists and agriculturalists) and the general social climate around questions of "progress" in the late nineteenth century.

Finally, moving beyond the case of reversion itself, I'll close by offering some general thoughts on the ways that a scientific problem might cease to be viewed as a problem. Both Thomas Kuhn and Larry Laudan, in their own quite different ways, considered the disappearance of scientific problems to be a particularly important factor in scientific change, and I will consider their views using atavism as a lens.

One clarification is particularly important before I continue. Authors throughout this period (and, following their choices of vocabulary, a number of historians of biology and statistics) have often moved back and forth between several of the different synonyms for reversion that I mentioned above, and also between (at least) two distinct things to which those terms might refer.

In what follows, I will use *reversion* to refer to *a biological phenomenon*: the reappearance of characters from remote ancestors in their descendants. It is important that we contrast this with (from Galton's invention of the technique onward) *regression*, which I will use to denote *a measurement technique*: the statistical tool that lets us argue that, to quote Galton's favored example, the height of children would be on average two-thirds as far from the mean as the height of their parents. Things become only more complex as regression is generalized as a statistical technique, including the calculation of regression coefficients not only between parent and offspring populations, but also between a population and its more remote descendants.

In some sense, the slippage between these two notions is entirely understandable: as I will discuss below, Galton invents regression, in part, to study reversion. But keeping the two concepts clearly separated will let us see facets of this debate that have yet to be noticed in the historical narrative for this period. While the techniques of regression entered into statistical and biological practice for good, the phenomenon of reversion that initially spurred research interest into those techniques quite swiftly ceased to be an important question for the evolutionary sciences. It is in that sense that I want to claim that reversion *ceased to be a scientific problem*: a phenomenon that was once taken to be one of the central explanatory targets of any theory of heredity became at best a curiosity, and at worst a misleading artifact of other processes of inheritance.

1. The Interest in Reversion

The concept of 'reversion,' or, under different guises, 'atavism' or (occasionally) 'regression' has a long history. As Staffan Müller-Wille and Hans-Jörg Rheinberger, among others, have argued, over the course of the eighteenth and early nineteenth centuries it emerges as practices of animal and plant breeding become more rigorous (2012, p. 65). They go on to note, however, that "institutional and social barriers prevented the development of a unified perspective on inheritance until well into the nineteenth century" (2012, p. 66). By the time Charles Darwin begins his investigation of heredity and common descent in the middle of the 1800s, reversion is front and center.

1.1. Charles Darwin

Darwin seems to become particularly interested in reversion to ancestral characters once he starts studying questions of breeding and artificial selection around 1856. Reversion, he realizes, can offer us a rare window into the prehistory of our domestic varieties – in particular, it can provide evidence that a number of apparently different domestic productions could in fact trace their ancestry to the same single wild species (Geison, 1969, p. 388).

The result of the evidence he accumulates prior to the drafting of the *Origin* is at this point quite familiar.[1] In particular, he is struck by the occasional appearance (in, it seems, both his own experience and that of other breeders), even among quite derived fancy pigeons (figure 1), "of slaty-blue birds with two black bars on the wings, a white rump, a bar at the end of the tail, with the outer feathers externally edged near their bases with white" (Darwin, 1859b, pp. 159–160) – that is, of birds that look for all the world like garden-variety wild pigeons. Darwin takes this as nigh-irrefutable evidence that all fancy breeds must be able to trace their descent back to the rock pigeon.[2] "I presume," he writes, "that no one will doubt that this is a case of reversion, and not of a new yet analogous variation appearing in the several breeds" (Darwin, 1859b, p. 160).

He goes further, however, noting that "it is a very surprising fact that characters should reappear after having been lost for many, perhaps for hundreds of generations,"

[1] I lack the space here to consider the differences between Darwin and Wallace on this point, visible even in the first paper from Wallace that spurs the publication of the *Origin*; see an illuminating discussion in Gayon (2016, pp. 169–171).

[2] For a detailed account of Darwin's relationship to pigeon breeding, see Secord (1981).

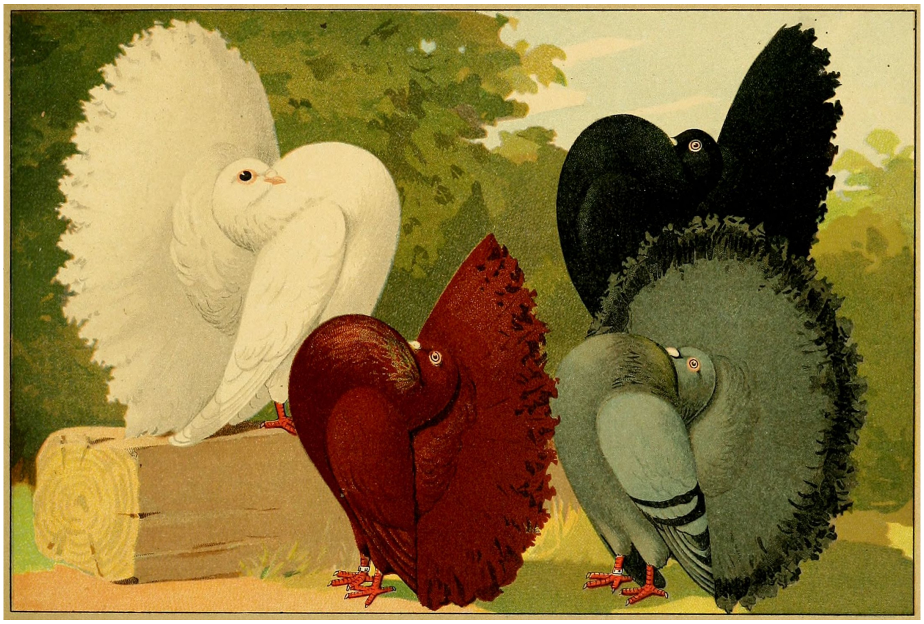

Figure 1: An illustration of highly derived "fantail" pigeons, from Emil Schachtzabel's *Illustriertes Prachtwerk sämtlicher Taubenrassen* (1906).

particularly given that, as the proportions fall off geometrically, "after twelve generations, the proportion of blood, to use a common expression, of any one ancestor, is only 1 in 2048; and yet, as we see, it is generally believed that a tendency to reversion is retained by this very small proportion of foreign blood" (Darwin, 1859b, p. 160). We should, then, be on the lookout for a physiological explanation that could account for the way in which such characters have been preserved over such a long period.

> When a character which has been lost in a breed, reappears after a great number of generations, the most probable hypothesis is, not that the offspring suddenly takes after an ancestor some hundred generations distant, but that in each successive generation there has been a tendency to reproduce the character in question, which at last, under unknown favourable conditions, gains an ascendancy. (Darwin, 1859b, p. 160–161)

Darwin hastens to add that he has no idea how this process might in fact work in the details, though it seems to him that the various facts he has offered us in favor of reversion allow for no other possible kind of explanation. As Darwin summarizes the state of his thinking in a letter to Joseph Dalton Hooker from May of 1859,

> With respect to reversions; I have been raking up vague recollections of vague facts; & the impression on my mind is *rather* more in favour of reversions, than it was when you were here.— In my abstract [i.e., the *Origin*] I give only a paragraph on the *general* case of reversions, though I

> enter on detail on some cases of reversions of special characters. (Darwin, 1859a)

For the Darwin of the *Origin,* reversion enters our field of view as a way in which we might begin to understand the deep past of our domestic productions, and offers in this vein a bit of useful evidence that he adds to his discussions of the principle of common ancestry.

But as Darwin moves from the *Origin* to the early drafting of *The Variation of Plants and Animals Under Domestication*, the topic becomes much more interesting to him. Gerald Geison notes that Darwin engages in a serious program of research into reversion over the intervening years – of the approximately seventy sources that Darwin references in his discussion on reversion in the final text of the *Variation*, more than thirty of them were published between 1859 and 1865 (Geison, 1969, p. 389, n.). By 1863, for example, he has already begun to structure his thoughts around the concept of latent transmitted characters. As he writes to Hooker,

> this view of latency collects a lot of facts—both secondary sexual character in each individual—tendency of latent character to appear temporarily in youth—effect of crossing in educing latent character &c.— When one thinks of a latent character being handed down hidden for a thousand or ten-thousand generations & then suddenly appearing, one is quite bewildered at the host of characters written in invisible ink on the germ. (Darwin, 1863)

Hooker agrees – offering Darwin "a thousand thanks for your explanation about Reversion in which I am sure I shall go the whole hog with you; it is a subject on which I have a huge *latent* interest" (Hooker, 1863, orig. emph.).

In May of 1865, three years before the publication of the *Variation*, Darwin prepares a manuscript called "Hypothesis of Pangenesis," which he later sends to T.H. Huxley for comments – before he has received any of the well known criticisms of the *Origin* by reviewers like Fleeming Jenkin (Hull, 1973). At this point, Darwin is beginning to see the phenomenon of reversion as the central concept around which he can explain all phenomena of *non-inheritance* – that is, the apparent failure of offspring to resemble their parents might be reinterpreted as the reemergence of ancestral characters. His early thought is worth quoting at length, if only to demonstrate the extent to which these ideas were worked out independently of his other responses to critics of the *Origin*:

> Other [than variation induced by the conditions of life], perhaps all other, cases of non-inheritance, may be included under the principle of Reversion, by which the child tends to resemble its grandfather or more remote progenitor rather than its parents.
>
> This principle of Reversion is the most wonderful of all the attributes of Inheritance. It frequently comes into action. What can be more wonderful than that characters, completely lost during scores or hundreds or even thousands of generations, should suddenly reappear perfectly developed. . . .

> We are led to believe ... that every character which occasionally reappears through reversion, is present, though latent in each generation.... In every living creature we may feel assured that a host of lost characters lie latent and ready to be evolved under the proper conditions. How can we make intelligible and connect with other facts this wonderful and common capacity of reversion – this power of apparently calling back to life long lost characters? (Olby, 1963, pp. 256–257)

The answer to this last rhetorical question is, of course, his hypothesis of pangenesis. Not all of the gemmules that an organism bears will be expressed in any particular generation; some will be latent in precisely the way that Darwin describes here. Their number, in turn, will be large enough that latency could reach back a vast number of generations into the past.

This discussion – with added references to the work of Charles Naudin, about whom more in the next subsection – persists in the final version of the *Variation*. Darwin writes there that "reversion, in the ordinary sense of the word, acts so incessantly, that it evidently forms an essential part of the general law of inheritance" (Darwin, 1875, p. 2:394). Darwin adds evidence that it appears to work across all parts of the plant and animal kingdom, and without regard to the mode of growth or reproduction of a species, though he does offer examples not only of confirmed cases of reversion, but also of cases where it would be expected but has not been observed (Gayon, 2016, p. 171–172). In the end, however, his explanation for these cases returns to pangenesis. All that is required for reversion to be possible is "the transmission from the forefather to his descendants of dormant gemmules, which occasionally become developed under certain known or unknown conditions" (Darwin, 1875, p. 2:399). In an analogy to which Galton will return in a number of years, he describes the interplay between these latent and expressed characters by comparison "with a bed of soil full of seeds, some of which germinate, some lie dormant for a period, whilst others perish" (Darwin, 1875, p. 2:399).

1.2. Darwin's Sources

In his immediate aftermath, Darwin himself proves to be the most important source on this topic. But two authors whom Darwin certainly read – Herbert Spencer and, as mentioned above, Charles Naudin – deserve brief mention as also having discussed questions of heredity and reversion in relevantly similar ways.[3]

Spencer. Prior to the publication of Darwin's thought on pangenesis, Herbert Spencer wrote skeptically in his *Principles of Biology* that "a positive explanation of Heredity is not to be expected in the present state of Biology" (Spencer, 1864, p. 1:253). That said, we can simplify the question, he argued, by drawing analogies between heredity and hypotheses covering other biological phenomena. To that end, Spencer briefly explores the idea that hereditary material is made from the same "physiological units"

[3] Churchill (1987, p. 342) also mentions Prosper Lucas as another author who had dealt with reversion and who was cited by Darwin in the *Origin*, a further source that I unfortunately lack the space to pursue here.

that construct the other parts and tissues of organized beings, with "the likeness of any organism to either parent ... conveyed by the special tendencies of the physiological units derived from that parent" (Spencer, 1864, p. 1:254). This is commonly cited as the source of the contemporary fascination with physiological theories of the units of inheritance (e.g., Froggatt and Nevin, 1971b, p. 15).

Spencer briefly deals with the phenomenon of reversion, under the name of atavism, writing that it is "proved by many and varied facts" (Spencer, 1864, p. 1:252), but refers back only to Darwin's examples of distant reversion in pigeons, drawn from the *Origin*.

Naudin. Darwin approvingly cites in his discussions of reversion a study on hybridism published by Charles Naudin, the second part of which appeared (paradoxically) in 1863, followed by the first part in 1865 (Naudin, 1863, 1865). As Naudin writes,

> Starting in the second generation, the physiognomy of hybrids is altered in a most remarkable way. Very often, the uniformity of the first generation which had been so perfect is succeeded by a motley variety of forms, some coming closer to the specific type of the father, others to that of the mother, some returning quickly and entirely to one or the other. (Naudin, 1863, p. 190)[4]

Why, then, would these reversions take place? Naudin proposes a physiological hypothesis:

> A hybrid plant is an individual where one finds united two different essences, each having their mode of vegetation and their own final cause, which mutually clash and are in unceasing struggle to free themselves from one another. [...] The hybrid, on this hypothesis, is a living mosaic, of which the eye cannot discern the discordant elements as long as they remain mixed.... (Naudin, 1863, pp. 191–192)

Hybrid plants, that is, form a sort of unstable mixture of two "essences," each of which aims constantly to triumph over the other. The observation of reversion back to a parental form after one generation of hybridity, then, would be straightforwardly expected on a view such as this.

In the notes enclosed with his copy of the first part of Naudin's work, Darwin described this work as "good on Hybrids being a living mosaic of 2 species," but as he notes in the margin of his copy of the second part, "this view will not account for distant reversion" (cited in Olby, 1966, p. 66). As he puts the objection more thoroughly in a letter to Hooker,

> I am glad that [the botanist George Bentham] is cautious about Naudin's view, for I cannot think that it will hold. The tendency of hybrids to revert to either parent is part of a wider law (which I am fully convinced that I can show experimentally) namely that crossing races as well as species tends to bring back characters which existed in progenitors, hundreds &

[4]Translations from the French are my own.

> thousands of generations ago. Why this should be so, God knows— But Naudin's view throws no light, that I can see, on this reversion of long lost characters. (Darwin, 1864)

Naudin thus feeds into Darwin's preoccupation with reversion, but offers us a fairly limited picture of single-generation reversion in hybrids (and, particularly, in plants).

1.3. August Weismann

For Weismann, one of the most important theorists of heredity and evolution to publish in the years immediately following Darwin, the question of reversion was intimately connected with natural selection. On Weismann's view, natural selection is the most powerful force shaping species in the wild – which naturally leads one to wonder what happens to species when a selective pressure is absent for a particular feature. In these cases, Weismann describes what occurs (in an unfortunate reuse of terminology that carries several other meanings elsewhere) as *panmixia* (Gayon, 2016, pp. 175–178). Without natural selection to cull the unfit, "all individuals can reproduce themselves and thus stamp their characters upon the species, and not only those which are in all respects, or in respect to some single organ, the fittest" (Weismann, 1891, p. 91). In these cases, crossing with less fit organisms can only serve to lower the fitness of the species in question, "which must in the course of time result in the deterioration of the average development of the organ" (Weismann, 1891, p. 299). It is important to underline that this sort of degeneration is not necessarily reversion to an ancestral type, and thus bears only an uncertain relationship to Darwin's cases of reversion. It is perhaps better understood as an explanation for evolutionary trends which appear to decrease complexity, which Darwin had predominantly ascribed to the inheritance of use and disuse.

In a different vein, in his widely read development of the theory of the continuity of the germ plasm, Weismann also proposed a theory of latent characters, here with the intent to explain phenomena much closer to reversion as discussed thus far. "It is obvious," he wrote, "that the nucleoplasm of each antecedent generation must be represented in any germ nucleus in an amount which becomes less as the number of intervening generations becomes greater," and in a simple geometric proportion, "calculated after the manner in which breeders ... determine the proportion of pure blood which is contained in any of the descendants," he produced the familiar $\frac{1}{2^n}$ fractional series. Even in the case of a fraction as small as $\frac{1}{1024}$, however, he writes that we must acknowledge that such a small proportion "can, nevertheless, exercise influence over the development of the offspring, for the phenomena of atavism show that the germ-plasm of very remote ancestors can occasionally make itself felt, in the sudden reappearance of long-lost characters" (Weismann, 1891, p. 182). We have, he writes, no theory that can actually explain how this works – but at least the continuity of the germ plasm can give us a way to see how it might be possible.

1.4. Francis Galton

Francis Galton must occupy a pivotal role in any discussion of reversion, if only because it is in his works that we first find the distinction that I labelled in the introduction one between *reversion* and *regression*. Galton develops techniques for the statistical exploration of population phenomena for a wide variety of reasons, much too rich for me to do full justice to in the present context (interested readers may consult Bulmer, 2003; Pence, 2022, ch. 2). But an important factor for Galton – present from his earliest works straight through to his last books on evolution and heredity – would be the importance which he gave to providing an explanation of reversion.

The origins of Galton's deep interest in ancestry and reversion – which he would later quantify as the Law of Ancestral Heredity – are, in fact, rather mysterious, and likely tied up in his lifelong belief in eugenics. Galton is already thinking about the question of the relationship between characters in the current generation and characters in (possibly quite distant) ancestors in 1864, when he drafts a pair of papers on "Hereditary Talent and Character" that would appear in 1865 (Galton, 1865a,b), some of his very earliest work on biological questions. From these earliest papers, focused as they were on extracting insights on the heredity of mental ability among the British upper classes (material that would go on to form his book *Hereditary Genius*), Galton is already preoccupied with reversion:

> Lastly, though the talent and character of both parents might, in any particular case, be of a remarkably noble order, and thoroughly congenial, yet they would necessarily have such mongrel antecedents that it would be absurd to expect their children to invariably equal them in their natural endowments. *The law of atavism prevents it.* (Galton, 1865b, p. 319, emph. added)

His early theoretical work attempting to provide explanations for these patterns of inheritance reads as though it could have been constructed on the basis of Darwin's pangenesis – but, recall, we are still around a year and a half before Darwin begins to distribute his first pangenesis sketch.[5] Galton's early engagements with pangenesis itself, after Darwin publishes it in the *Variation*, also directly tie part of that theory's importance for him to the phenomena of reversion. One of the most attractive features of pangenesis, he writes, is "that gemmules of innumerable varieties may be transmitted for an enormous number of generations without being developed into cells, but always ready to become so, *as shown by the almost insuperable tendency to feral reversion, in domesticated animals*" (Galton, 1871, p. 394, emph. added).[6]

What, then, was Galton's proposal? Over the course of the 1870s, Galton's work would move in two directions. On the one hand, he would thoroughly explore the evidence for the phenomenon of reversion, and he would refer to them in his publications for the rest of his career (e.g. Galton, 1889, p. 189). And on the other hand, he would also introduce the statistical measure of regression – first as a way to capture reversion, and then, as he and others would quickly realize over the ensuing years, as a much broader and more general inferential tool. Throughout, Galton's would still place a strong emphasis on the idea that (however operationalized or formalized) some

[5] There is no hard documentary evidence that Galton had been given a "preview" of Darwin's theory; it is probably, therefore, safest to take Galton at his word that he arrived at his conclusions through a sort of *a priori* reasoning which he would discuss several times over the next few decades (Froggatt and Nevin, 1971a; Bulmer, 1998; Pence, 2022, ch. 2).

[6] A similar discussion occurs in Galton (1869, p. 370).

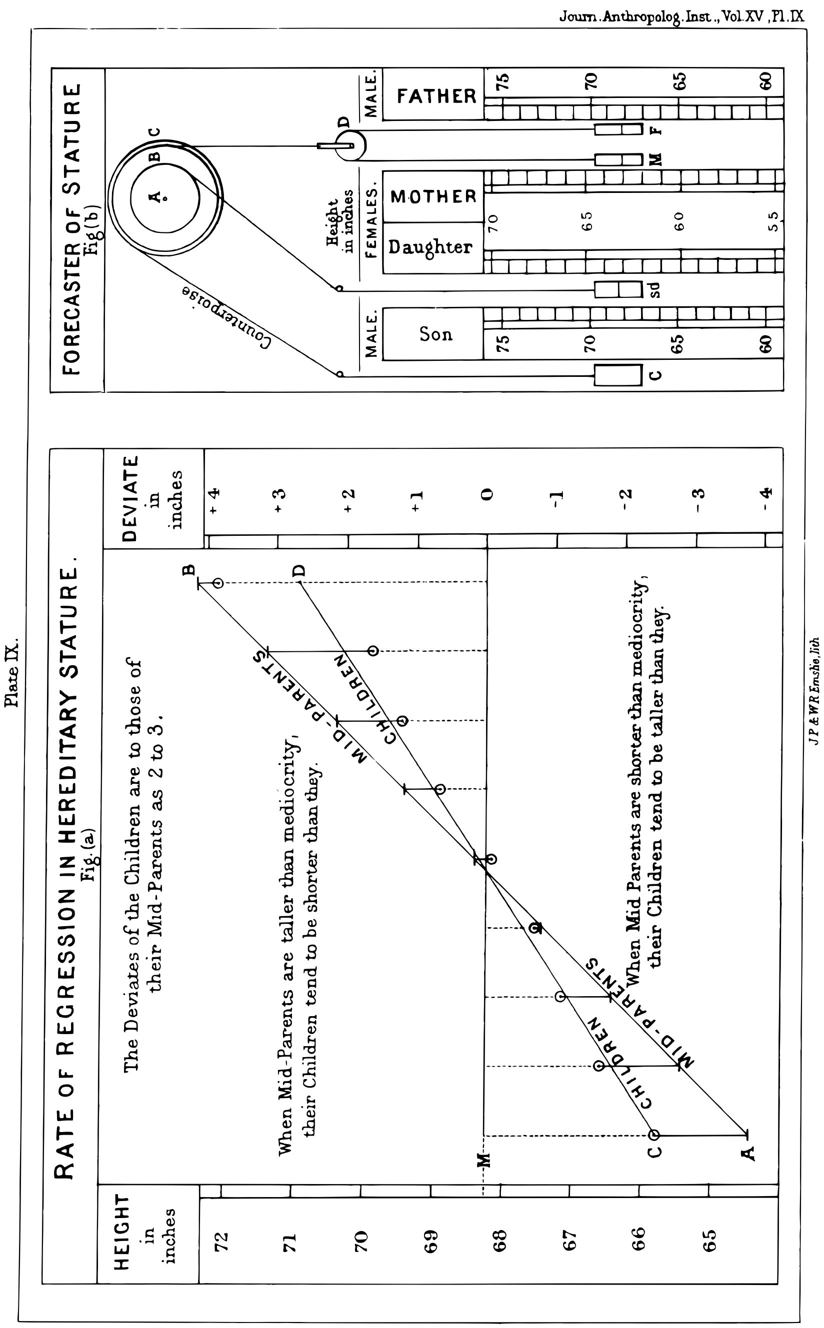

Figure 2: The line of regression of the height of offspring on parents, along with Galton's physical model he designed to predict child heights from the heights of the parents. From Galton (1886).

sort of preservation of a fraction of gemmules from distant ancestors was necessary to explain the phenomenon of reversion. To begin to understand how these concepts are interrelated for Galton, let's move forward to the mature statement of his views that we find in his 1885 Presidential Address to the Anthropological Section of the British Association. The data behind the address, along with some expanded arguments, were published the following year (Galton, 1886).

His primary goal in this lecture was to describe his measurements of the statistical regression of the height of offspring on the height of parents (see figure 2). Consider a particularly extreme (in the sense of being far from the mean value in the population) pair of parents, or, to borrow Galton's terminology, a particularly extreme *mid-parent*, the average of the two parents. We will find that, on the average, the heights of their offspring will be less extreme than their own – and they will be less extreme in a constant proportion, one which Galton estimated to be approximately $\frac{2}{3}$.

Why would this be so? In fact, Galton argues, we should have expected it:

> The child inherits partly from his parents, partly from his ancestry. Speaking generally, the further his genealogy goes back, the more numerous and varied will his ancestry become, until they cease to differ from any equally numerous sample taken at haphazard from the race at large. Their mean stature will then be the same as that of the race; in other words, it will be mediocre. Or, to put the same fact into another form, the most probable value of the mid-ancestral deviates in any remote generation is zero. (Galton, 1886, pp. 252–253)

Put differently, we can imagine two extreme cases for the operation of inheritance, both of which clearly don't occur in nature. On the one hand, parents could simply produce carbon copies of themselves as their offspring. In that case, the deviation of offspring from the mean would be identical to the deviation of their parents from the mean – and the regression of offspring on parents would be equal to 1 (offspring would be exactly as extreme as their parents). On the other hand, imagine that offspring inherited nothing from their parents, and only took on characters drawn from distant ancestors. Galton notes that, since distant ancestors amount to, in essence, a random sample from the ancestral population in general, the mean value of any character in one's collection of distant ancestors just *is* the mean value for the entire population as a whole – and the regression of offspring on parents would be equal to 0.

However, we know – though Galton does not tell us *why* we know, other than relying on the same kinds of intuitions that Darwin had and his extant general belief in the importance of explaining reversion – that children inherit their characters partly from their parents, and partly from their more distant ancestors. Thus, we should have predicted in advance that the regression of offspring on parents would be somewhere between the implausible extremes of 0 and 1 – and empirical observation confirms that it is $\frac{2}{3}$.

It is in the appendix to this same paper that Galton offers his first clear derivation of the law of ancestral heredity – his mathematical formula for the proportion in which each particular ancestor would have contributed to the character of the current generation. In a rather incoherent methodology for building a novel theory, he offers us two derivations of the law – each mutually inconsistent, derived from differing presuppositions – and then averages their resulting numerical constants, resulting in a simple geometric series, with the mid-parent contributing $\frac{1}{2}$ of the offspring's characters, the mid-grand-parent $\frac{1}{4}$, and so forth.

Many articles have been devoted to the law of ancestral heredity (see, e.g., Swinburne, 1965; Froggatt and Nevin, 1971b,a; Bulmer, 1998; Magnello, 1998; Gayon, 1998). Galton derives it in a wide variety of incompatible (and, one is tempted to say, often incomprehensible) ways.[7] More interestingly, the precise nature of his commitment to the law is quite unclear. Contra Karl Pearson (to whose view we will turn shortly), it appears as though Galton thought of the law as "both a representation of the separate contributions of each ancestor, on average, to the heritage of the offspring and as a prediction formula for predicting the value of a trait from ancestral values" (Bulmer, 1998, p. 580) – that is, Galton thought of the law both as a physiological description of the process of particulate heredity as it actually occurs, and as a statistical predictor, perhaps not even seeing the difference between these two ways of considering the law.[8]

Galton revisits the law once more in 1897, in one of his last real contributions to the study of heredity.[9] Arguing now that it is "universally applicable to bisexual descent," he uses data from coat colors in basset hounds to demonstrate it (Galton, 1897, p. 401). In general, he appeals (somewhat oxymoronically) to "a wide though limited range of observation," which "assures us that the occupier of each ancestral place *may* contribute something of his own personal peculiarity, apart from all others, to the heritage of the offspring" (Galton, 1897, p. 403), and that contributions from more distant ancestors are rarer than those from closer. Finally, since the series of proportions must sum to 1 (and thus account for the entire heritage of the offspring), "the law might be inferred with considerable assurance *à priori*; consequently, being found true in the particular case [of the basset hounds], there is good reason to accept the law in a general sense" (Galton, 1897, p. 403).

Meanwhile, Galton has developed a parallel description of the physiological basis of heredity – the 'stirp' – that could support this significant role for distant reversion. Galton attempts to offer us a theory of the material underpinnings of heredity that can account for long-term latent characteristics and observed statistical patterns of inheritance, without committing itself to any particular details about the underlying physical process that could lead his theory into the same kind of trouble that had befallen Darwin's theory of pangenesis (at Galton's own hand; see Galton, 1871). As he puts it, "I have largely used metaphor and illustration to explain the facts, wishing to avoid entanglements with theory as far as possible, inasmuch as no complete theory of inheritance has yet been propounded that meets with general acceptation" (Galton, 1889, p. 34).

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[7] Thankfully, the details of these various derivations are not important for our purposes here.

[8] As Gayon puts it when describing this aspect of Galton's work, "the whole of Galton's method required that heredity, like selection (in both its elements – survival and fertility), should conform to the 'law of deviation' (the normal law)" (Gayon, 1998, p. 157). I disagree with Gayon's claim that Galton renounced this approach to the problem after 1885, though I lack the space to pursue that disagreement here.

[9] Galton would spend the last decade of his life doing little more than publicly arguing for eugenics in Britain.

In short, his picture of inheritance says only that inheritance occurs by the passing of innumerable particles from the germ-line cells of parents to those of offspring, some of which are latent and some of which are patent. It shares these features with Darwin's pangenesis, but strips Darwin's theory of any implication about the movement of particles through cells, their accumulation in the reproductive organs, and in particular (in accord with another of Galton's theoretical convictions) with no role to be played by the inheritance of acquired characters. The very structure of this particulate theory is built, then, with the law of ancestral heredity in mind – the large number of these particles, and their transmission from germ-cell to germ-cell unchanged, encourages us to think of their long-term fates in exactly the way we would expect given Galton's extensive engagement with reversion and ancestral contribution.

So much for Galton's having made room in his theory for the phenomenon of reversion. The story of regression is somewhat different.[10] Having initially thought of regression as a way to quantify the extent of reversion, he only later realized that, just as one may compute the regression of offspring on parents, one may *also* compute the regression of parents on offspring – the mathematical approach here is entirely symmetrical.[11] In this case, to be sure, regression cannot be a simple measure of reversion to characteristics of ancestors – the tight link that Galton had sought between them was broken, and regression took on a life of its own as a fundamental concept for the development of modern statistics. We will not consider it further here.

1.5. The Biometrical School

The question of reversion was equally poignant to Karl Pearson and W.F.R. Weldon, the two figures most central to the pursuit of biometry, the mathematized, statistical development of evolutionary theory which flourished from 1890–1906. A full exploration of this concept across all their works would take me too far afield here, so I want to focus on two particular instances: the discussion of the law of ancestral heredity and the so-called *law of reversion* that Pearson deploys in his *Grammar of Science*, a synthetic presentation of his views on evolution published in 1900; and the way in which this notion would find itself expressed in the later work of Weldon in 1905 and 1906, as he struggled to square the statistical approach to evolutionary biology that he and Pearson had developed with the advent of Mendelism.

Over the last few years of the nineteenth century, Pearson had endeavored to figure out just how Galton's law of ancestral heredity should be understood. As more and more statistical data was collected, and more correlation and regression coefficients between organisms and their relatives were derived, Pearson had begun to realize that the simplistic approach of Galton – on which every single trait owed its presence in the organism to its identical presence in some particular ancestor – was too limiting. Most problematically, it entailed that we *must* have mutations in these characters if we are to see genuine novelty (rather than just novel recombination). Galton, for his part,

[10] My treatment of the statistical tools of regression must be brief here for reasons of space and emphasis. For illuminating discussions of this technical apparatus, see Stigler (1986, pp. 294–297), Porter (1986, pp. 286–296), and Bulmer (2003, pp. 184–196).

[11] Failure to recognize this was something of which Pearson would later regularly accuse Bateson and his colleagues, for instance (Pearson, 1902, pp. 322–323).

had been persistently confused on the question of whether evolution proceeded only gradually, or by fits and starts (i.e., the question of saltationism; see Bowler, 2014). Pearson, a through-and-through gradualist, brooked no such confusion.

His approach, developed first in two papers (Pearson, 1898, 1900b) and then presented for a broader audience later that year (Pearson, 1900a), was to separate the law of ancestral heredity as a description of a different kind of phenomenon than the *law of reversion*.[12] This is not so different from Galton's progressive realization that regression applied to more than just the concept of reversion, as we see Pearson attempting to understand the law of ancestral heredity not with reversion in mind (as Galton had done), but through the lens of regression.

For Pearson, the law of ancestral heredity – the evidence for which would consist of examining the correlations between organisms and their ancestors – could only apply in cases of blending inheritance, where character values are statistically distributed, as only here do we have any correlations with which to work in the first place. In these cases, he writes, "every ancestor contributes, it may be, a very small share of his character to each offspring," and we have a phenomenon that should properly be termed *regression* (Pearson, 1900a, p. 495). In short, while Galton was right to divorce regression from reversion, Pearson thinks, he had miscategorized the law of ancestral heredity: this is a regression-based formula arising from blending inheritance, not a tool for explaining reversion by means of long-latent ancestral characters.

When characters are, on the contrary, transmitted by what Pearson calls *alternative inheritance* – that is, inheritance like that found in Mendelian characters, where one or the other of a pair of traits is expressed without blending in offspring – we could potentially have proper cases of *reversion*, on which "each ancestor contributes the full intensity of his character to his share, and it may be an indefinitely small share of the offspring" (Pearson, 1900a, p. 495). Mirroring his general skepticism about the utility of Mendelian patterns of inheritance, however, Pearson goes on to argue that he knows of no certain instance of reversion in this precisely defined sense: "Mr. Francis Galton's investigations on Basset hounds bring, indeed, evidence in favour ... but my own on eye-colour are not in good agreement" (Pearson, 1900a, p. 496).

By only a few years later, however, and facing an increasing number of what Pearson and Weldon took to be limited confirmations of genuine Mendelian inheritance phenomena, Weldon would set about a dramatically different project. As early as 1896 (Weldon, 1896), and with increasing frequency after 1900 (e.g., Weldon, 1902), Weldon began to be convinced that, (1) chromosomes were almost certainly the material bearers of hereditary material, (2) Galton's conception of that material basis as a 'stirp' bearing a vast number of latent and patent characters was the correct way to interpret chromosomal function, and (3) such a theory could produce both statistical, blending inheritance of the sort that the biometricians treasured as well as Mendelian transmission patterns as a special case.

For Weldon, then, Galton and Pearson's separation of reversion from regression proves too much – strongly separating alternative from blending inheritance in this

[12]See also Gayon (2016, pp. 181–182) for discussion of a related aspect of Pearson's work on reversion from a few years prior.

way (and arguing that most of biometry's analytical tools apply, in turn, only to cases of blending inheritance) would prevent Weldon from making Mendelism appear as a special case of biometry. He wrote to Pearson in early 1905 that "the thing that has been worrying me is Galton's theory of reversion." Repeating what we have already seen in Pearson's case above, he continues a bit further on:

> [A]s you agreed some time ago, it is a necessary consequence of his view that the sum of the ancestral regressions should = 1, and you find that in fact that they do not, at least if you extrapolate your series backwards as a [general principle].
>
> Now if you suppose that individual determinants are not transmitted without variation, but that similar determinant elements acquire a sensible [standard deviation] in passing say from the body of one generation to that of another, you diminish all the ancestral correlations, and therefore the sum of all of them, and the "contribution of the ancestry" no longer constitutes *all* the characters of the generation. [...] But one ought to be able to calculate the relation between possible values of such [standard deviations] and your values for correlation and regression, and of course such an effort is beyond me. (Weldon, 1905, f. 1–2)

Weldon starts by recognizing (here, agreeing with Pearson) that Galton's view of the law of ancestral heredity is going to give values for regression coefficients that don't line up with Pearson's empirical data. He then offers us a proposal for what a more general theory than Pearson's might look like: if we begin with Galton's stirps, but we introduce a process that increases variance in transmission over generational time, we could add another free parameter to the model – one that, Weldon hoped, we might vary so as to produce Mendelian inheritance in some cases, and biometrical inheritance in others.

Because the mathematical analysis that incorporated this kind of variation among the elements was too complex for his statistical ability, Weldon began by setting out simply to understand the relationship between parental and offspring character distributions with exact transmission. He never finished this effort, dying prematurely in 1906 after a short illness.

2. The Rejection of Reversion

As I noted in the introduction, however, reversion ceased to be a central focus for evolutionary science – in the limited sense in which I've used it here, ceased to be a scientific problem – just as quickly as it had become one. Over the first few decades of the twentieth century, its stock fell dramatically.

At least some opposition to the notion of reversion gathered steam even earlier. William Bateson wrote in 1894 that "around the term Reversion a singular set of false ideas have gathered themselves," claiming that reversion was nothing more than a way of explaining "the discontinuous occurrence of new forms possessing such perfection and completeness" on a gradualist view of evolution (Bateson, 1894, p. 76). For him, reversion is merely an accident – just as with all "statistical examination of ancestral composition," he would write later in a 1909 textbook, we may "occasionally give a prediction in good correspondence with fact, but this is due to coincidence and not to any elements of truth in the ratiocination by which the prediction was reached" (Bateson, 1909, p. 131). Such coincidences might sometimes be called reversion, "when the sum total of the factors returns to that which it has been in some original type" (Bateson, 1909, p. 279).[13]

As an aside, it is worth noting that the issue of reversion was thus absorbed into the broader "biometry-Mendelism" debate, which pitted those (like Pearson and Weldon) arguing for the gradual nature and statistical treatment of evolutionary change against those (like Bateson) who argued for discontinuous change of Mendelian characters driven by mutation (among other portions of a vast literature, see Provine, 1971; MacKenzie, 1981; Bowler, 1992; Kim, 1994; Gayon, 1998; Porter, 2004; Cock and Forsdyke, 2008). I am not certain, however, that this is the obvious framework with which to approach the question of reversion.[14] As we have seen, Weldon takes reversion very seriously and Bateson rejects it. But Pearson has an interestingly mixed opinion, and Galton – who was taken to be "above the fray" of this debate and never took a clear side, despite his apparent affinity with the biometricians (Bulmer, 2003, p. xvii) – believed it to be a serious problem.

On the broader scale, it is more difficult to clearly chart the disappearance of reversion from the literature, just as it is generally difficult to prove a historical negative. As we move into the late 1920s and 1930s, it is widely known that the architects of the Modern Synthesis *didn't* talk about a lot of different phenomena or concepts from the prior history of biology, and only very rarely did they remark upon their omissions.

A few signals, however, can be found. First, we can hunt for the concept in the works of the major authors of the early Synthesis. R.A. Fisher's most closely related work to questions of ancestry, for instance, in which he reconstructs the same correlations that Pearson took to be evidence for the law of ancestral heredity on the hypothesis of Mendelian transmission (on many accounts, starting in the process the Modern Synthesis; Fisher, 1918), does not mention reversion or atavism directly as a phenomenon to be saved.[15] His concern is rather with the values of correlation coefficients found between each of the generations at issue – that is, with the more sophisticated mathematical and statistical apparatus that Pearson had constructed (via generalizing Pearson's requirement that the dominance at issue in Mendelian inheritance be complete).

In his *Genetical Theory of Natural Selection*, Fisher only mentions the phenomenon of reversion as one of the problems which faced Darwin, "a fact which stood outside his scheme of inheritance" (Fisher, 1930, p. 6), and (later in his section dedicated to the prehistory of genetics) as a problem that could be solved by a naive Mendelian ap-

[13]Of course, this description of reversion – as the fortuitous combination of a precise set of characters (now in a Mendelian sense) that were once united in a remote ancestor – could describe similar phenomena in a way entirely consistent with today's genetics as well. I thank Philipp Haueis and Rose Trappes for encouraging me to make this point clear.

[14]In that sense, I join authors such as Shan (2020) who have begun to question the reasonableness of the stringent biometry-Mendelism frame for understanding this period.

[15]Neither does Fisher's later foundational paper (1922), nor either of the two most famous early works of Sewall Wright (1929; 1931).

proach with simple dominance holding among a large number of genes, on which "every union of two heterozygotes will then produce among the offspring some recessives, differing in appearance from their parents, but probably resembling some grandparent or ancestor" (Fisher, 1930, p. 9).

A similar view of the field is obtained from textual analysis of the journal literature during this period. To take only two broad and fairly representative examples, full-text search of the journals *Nature* and *Proceedings of the Royal Society B* (containing its biological content) indicates that from the late-nineteenth century until around 1910, the terms 'reversion' or 'atavism' appeared in around 1.5% of all published journal articles. After 1910, this falls drastically to 0.5% and remains there until the present.[16] Such an analysis is of course not conclusive, but it is entirely in line with the rest of the story here.

Lastly, a few authors did indeed explicitly discuss the fate of reversion on the now-accepted Mendelian or early-Synthesis theory. One such was T.H. Morgan, who in 1905 argued that some of Lucien Cuénot's results on mouse coat color should offer a more complicated conception of latency than that proposed by the early Mendelians. "Pure" germ cells are not required for Mendelian theory, he notes – rather, "purity only means dominance over latency" (Morgan, 1905, p. 879). Thus the phenomena of latent characters and reversion are steadily being merged into broader discussions in the conceptual foundations of the budding science of genetics (a phenomenon I have noted elsewhere; see Pence and Swaim, 2018).

Perhaps more tellingly, in 1938 the anthropologist Ashley Montagu could write off the entire concept of atavism as though it was already a historical relic within the sphere of evolution – a notion which dates from "the days when biologists were sedulously engaged in supplying the finishing touches to the house that Darwin built," one that "abounds in the writings of nineteenth-century biologists" (Ashley-Montagu, 1938, p. 462). The idea persists, he argues, in some uncritical writings about man, but he concludes by writing that

> In short, it is more than doubtful whether the concept of atavism has any counterpart in reality; and, I think it will be agreed, that unless the concept can be applied to some demonstrable type of phenomenon, it were better that the term were altogether dropped from the vocabulary of the biologist. (Ashley-Montagu, 1938, p. 463)

Such an argument proves in the end to have been too hasty. Papers today still mention the concept of reversion or atavism, though again as a kind of curiosity, something to be explored in terms of genetic or developmental mechanisms producing specific characters in specific cases.[17] In any case, reversion is far from being the kind of question that could drive a research program in evolutionary theory, as it clearly had been for the authors that we have seen in the previous section.

[16] Analysis performed using evoText (Ramsey and Pence, 2016); data available at `https://doi.org/10.6084/m9.figshare.12594455`.

[17] Think, for instance, of the possibility of whales being born with a "reversion" to possessing hind limbs, as a result of particular kinds of normally-suppressed developmental mechanisms (Bejder and Hall, 2002). Thanks to Rose Trappes for the example.

3. The Rise and Fall of Reversion

So much for the empirical case. Reversion powerfully enters the discussion of evolution in the work of Darwin – first, as support for the common ancestry of domesticated products, and then, as Darwin moves to the *Variation,* as one of the central phenomena to be explained by any theory of inheritance. The question seems to be "in the air" at the time, as it is discussed by a variety of contemporary authors across Europe. Galton picks up on the question in turn, and, in a real sense, via the law of ancestral heredity, it structures his entire approach to the nature of heredity. His introduction of regression both reshapes our discussion of reversion itself and provides us with one of the foundational tools of population-level statistical analysis in the decades to come.

Looking forward, then, while there are a few references to the phenomenon in the first two decades of the twentieth century, it is already falling out of favor in the 1910s, and by the time the Modern Synthesis is fully put into motion, reversion is no longer a relevant fact about the natural world that theories in evolution or heredity need to explain. It is considered entirely outdated, to be consigned to the dustbin of history, well before the major textbook publications associated with the "hardening" of the Synthesis in the 1940s and 1950s, and the flurry of activity surrounding the "Darwin centennial" in 1959 (Gould, 1983; Smocovitis, 1996).[18]

It is thus high time to return to the question with which we began. Why did this happen? Why, that is, was reversion to characters of distant ancestors a phenomenon of vital interest in the first place, for authors from Darwin to Weldon – and then what made it lose this pride of place in the decades following?

3.1. A Few Other Alternatives

Before I detail my preferred explanation, we should consider several others already present in the literature. We should not, of course, expect a clear answer to be present in the primary sources; these authors only rarely recognized either that they were introducing an original theoretical category, or removing one from their lexicon. We are thus left with little choice but to speculate, drawing links between the rise of interest in reversion and a variety of other systematic questions, concerns, and problems present in mid-nineteenth century life sciences.

Of course, perhaps the most simplistic approach would be to say that at first, empirical results demonstrating reversion were novel, while later data simply stopped providing striking cases of distant reversion, and biologists naturally lost interest. Robert Olby, for example, notes that Darwin's examples themselves could be relatively quickly empirically dismissed just a few decades later. "Unfortunately," he writes, "the examples of distant reversion which Darwin cited were really due either to mutation, as in the case of polydactyly, or to genic interaction, as in the case of the wild-type plumage of pigeons" (Olby, 1966, p. 67). We might thus have at least a partial explanation for

[18] I unfortunately lack the space here to consider the way in which the older sense of reversion might interact with later debates on the *reversibility* of evolution – for instance, Gould's famous discussion of Dollo's Law (Gould, 1970).

the steady loss of interest in reversion. As what was once thought to be an unified empirical phenomenon was shown to be the result of a host of disparate causes, the need for reversion as a theoretical concept dried up.

This must be true in at least the trivial sense that the phenomena once brought under the category of reversion are now somehow explained in a different way – reversion in the sense we have discussed it here has been thus "left behind" by the march of empirical results.[19] As Fisher puts it, for instance, as we began to realize how many Mendelian characters are involved in the expression of many phenotypes, such an inheritance structure comes with the small but non-zero probability that hybridization can cause long-disappeared phenotypes to re-emerge (as quoted above in Section 2, Fisher, 1930, p. 9). But such a dismissal of reversion as a problem in general requires that the problem being dismissed is actually the one being treated in the positive accounts of reversion. It's not clear that we can make that claim here. A Fisher-style explanation of reversion is, to borrow a classic philosophical turn of phrase, to *dissolve* rather than *solve* the problem of reversion. If reversion is nothing more than a rare but nonetheless expected special case of Mendelian inheritance, then reversion has simply ceased to be a distinctive phenomenon in need of scientific explanation, ceased to constitute a scientific problem in the sense of the term I've used here. For Fisher, then, reversion is just not an issue, despite the fact that one might be able to see some apparently similar phenomena in a Fisherian lens. One senses in his rapid movement past it that reversion does not appear as a category in Fisher's world.

Another avenue for understanding reversion lies in the more general role of discussions between naturalists or life scientists and their colleagues in animal breeding and horticulture. As early as 1839, Darwin was sending some embryonic questions about reversion and atavism to correspondents such as the botanist William Herbert (Darwin, 1839). Jean Gayon has emphasized the fact that Alfred Russel Wallace considered the nature of domestic productions to be so unstable as to follow a different trajectory when released in the wild – unlike species in nature, a "return" to an ancestral state will necessarily occur (2016, p. 170). In general, as several authors have emphasized in recent years (Secord, 1981; Vicedo, 1995; Roll-Hansen, 2000; Hodge, 2009; Bowler, 2009; Radick, 2012; Gayon, 2016), reconstructions of Darwin and the response to Darwin have underemphasized or even ignored the important role of agriculture and breeding for providing source material, empirical data, and even for turning the tide in theoretical contexts (such as Bateson's advocacy of Mendelism as a practically useful tool). To gesture at only one way in which this might be relevant, we might think that reversion is a phenomenon that is salient only in the context of, as Andrew Mendelsohn put it for the case of vaccine production, "agricultural and other enterprises of biological stabilization and standardization in this period," which led to a "shift away from ambiguity and degree" (Mendelsohn, 2016, pp. 254, 255; note the contrast with Wallace's emphasis on *instability*). The focus on the creation of standard, commercializable breeds and

[19]The interpersonal element lying behind those empirical results is also not to be neglected – as Gregory Radick has noted (pers. comm.), one should not underestimate the power of mentors like Bateson telling their students that the kinds of problems, reversion included, that biometricians like Pearson and Weldon were interested in were simply not worth investigating.

strains was, plausibly, threatened by the possibility of reversion.[20]

While this was assuredly an important institutional and cultural development for the authors I have discussed (especially for Darwin and for Fisher, who spent his early years of scientific work at an agricultural station; Parolini, 2015), it's difficult to draw anything like a clear link here. Excepting perhaps Darwin's pigeons, there are no discussions of breed standardization or the development of agricultural strains in particularly close concert with discussions of reversion. The process of standardizing breeds was no less in effect in Fisher's day than it had been in Darwin's, and Fisher nonetheless rejects reversion. It seems as though we should keep searching for explanations.

Another common move in the history of the life sciences has been to connect worries about reversion or atavism with the theory of recapitulation. If one is committed to the idea that each individual organism lives out its own evolutionary history every time that development takes place, then reversion is an obvious, even expected occurrence, a result of occasional failures of elements of that process to reach their expected conclusions. As Ashley Montagu writes,

> Haeckel's Biogenetic Law really represents a generalized synoptic version of this concept [atavism] applied to a particular case, and calculated to resume a certain supposed routine of phenomena under a particular law. To-day few biologists believe that in its ontogenetic development any animal actually repeats the developmental stages of its phylogenetic history. (Ashley-Montagu, 1938, p. 462)

This theory gains some initial plausibility from the fact that, as we know, Darwin had some affinity for recapitulation (e.g., Darwin, 1859b, p. 338). But it offers us no explanation for the continued interest in the theory from authors like Galton, Pearson, and Weldon, who lacked any apparent interest in Haeckelian recapitulation.

Next, it's worth our while to pause to consider the relationship between reversion and blending inheritance.[21] In some sense or another (and as we have seen more or less explicitly above), Darwin, Galton, Pearson, and Weldon all shared a commitment to at least some form of (what they sometimes even themselves called) blending inheritance. Olby, for instance, frames a discussion of these same questions in Darwin, Naudin, and Galton not in terms of reversion, but rather around blending inheritance, which he calls "the most unfortunate of the assumptions underlying Darwin's mechanism of evolution" (Olby, 1966, p. 55). But there is something of a paradox here. Blending inheritance, as a theoretical commitment considered in isolation, seems to make reversion significantly harder to explain. If all characters blend, then the likelihood of reverting to the appearance of a distant ancestor seems small. So why would a group committed to blending inheritance have been the very same authors to be focused on reversion? Shouldn't they have attempted, as far as possible, to discount it, rather than repeatedly

[20]As an anonymous reviewer notes, it's also plausible that the quality of agricultural or breeding experiments might have improved over this period, such that the appearance of reversion might have become more rare as an observed outcome.

[21]I thank two anonymous reviewers for encouraging me to consider this point. For important context concerning the concept of blending inheritance during this time period, see (Porter, 2014).

emphasizing its importance, or as Pearson did, attempt to distance cases of blending inheritance from reversion *sensu stricto*?

Of course, as we have already noted, part of the explanation for this attachment to reversion has to do with appraisal of the empirical cases; it seems clear that all these authors took the demonstrations of reversion with which they were acquainted to be incontrovertible. But the lack of any effort to explain them away or minimize their importance seems to indicate that there were other reasons that also contributed to the importance that they gave to the phenomenon of reversion – in short, it seems to call for exactly the kind of broader analysis that forms my project here.

Finally, another long tradition in thought about heredity connects worries about reversion with concerns about the progressive spirit that animated so much of late nineteenth-century biology and eugenics – thus forming part of a trend that Gayon describes as "the general pessimism of European thought in the final third of the nineteenth century, a period in which, in almost all areas of culture, progressivist thinking was harshly criticized and challenged by declinist thinking" (Gayon, 2016, p. 181). At the most straightforward, practical level, reversion might be seen as something that thwarts our efforts at ameliorating hereditary diseases. As described by Bernd Gausemeier, the German historian and genealogist Ottokar Lorenz argued that

> proper genealogical method would enable scientists to demonstrate certain regularities of human heredity, particularly for what he considered to be its central question – the problem of latency or "atavism" … [which] seemed especially important to Lorenz because he regarded it as the main source for the modern "horror" of hereditary diseases. (Gausemeier, 2005, p. 183)

This, then, is reversion in service of a practical end – if most hereditary disorders are caused by bad "family types" reoccurring in later generations, then a thorough knowledge of them would enable us perhaps to stamp them out once and for all.

We can make the case more general, however, than the practical treatment of disease. Rather than a direct impact on society, we might see fear of atavism as more symbolic than practical. Reversion, on this view, represents a sort of vague bogeyman, the prospect that any progressive change we might make in human society could be wiped out at a single stroke by the return of long-dormant, atavistic characters. Marianne Sommer, for instance, writes that

> In the latter half of the nineteenth century until well into the twentieth, atavisms and their close relatives came to haunt philosophical, literary, sociological, and psychological discourses as the shady side of the progressionist paradigm. (Sommer, 2005, p. 234)

On this view, preoccupation with atavism is emblematic of a deeper cultural current. As Müller-Wille and Rheinberger put it, the past was an unwelcome guest in nineteenth-century discussions of heredity, and even when it appeared – atavism or reversion being a classic case – it represented a "threat to the present" (Müller-Wille and Rheinberger, 2005, p. 7). If this obsession with progress is a peculiarly nineteenth-century phenomenon, "symptomatic of a growing uncertainty" (Sommer, 2005, p. 234; see also Pick, 1989), the disappearance of reversion from biological discourse might be seen as, similarly, the signal of that uncertainty's waning over the early decades of the twentieth century. This explanation, however, runs afoul of the apparent lack of connection between support for eugenics and attention to reversion in the cases considered here. We have seen non-eugenicist "reversionists" (Darwin), eugenicist reversionists (Galton), eugenicist non-reversionists (Fisher), and non-eugenicist non-reversionists (Bateson). A focus on reversion and a feeling of "threat" or "uncertainty" simply seem not to be correlated with one another.

3.2. Philosophies of Biology

If none of the solutions thus far can offer us a general account of the rise and fall of reversion as a scientific problem, to what might we turn instead? I want to consider here the commitments to various kinds of broader, conceptual features of evolution held by each of these authors. The ways in which these more general commitments were made specific in the work of each, I argue, can help us uncover a new understanding of reversion's historical trajectory.

Let's begin with Darwin and Galton. One feature that both biologists believed was an essential component of evolution stands out: the gradual action of natural selection.[22] Darwin, spurred both by his Lyellian uniformitarianism (Hodge, 1983) and his Herschellian-Newtonian philosophy of science (Pence, 2018) fosters a picture of the world on which heredity should proceed not via drastic reversion to long-disappeared ancestors, but slow, steady steps that would be suitable for the action of natural selection. This was crucial for the "black box" sort of variation that Darwin and Galton both took for granted as the source of raw material for selection. The order of the day, as both often put it, is that "like begets like." The fact that reversion had become one of the central concepts of agricultural breeding over the early part of the nineteenth century (recalling, too, the extent to which Darwin was in close consultation with plant and animal breeders of his day) thus stood as an obvious problem for Darwin's picture of how his theory ought to operate.

Galton, for his part, also sees on the horizon the possibility that a particulate theory of inheritance could result in the mathematization of evolution and the accurate prediction of the characters of future generations from those in the present. His focus on such mathematical description is broadly predictive – consonant with his support of eugenics, a formalization of heredity would allow us to optimize future prediction and control of the living world. As he puts it, it "gives excellent materials for mathematical formulae, the constants of which might be supplied through averages of facts, like those contained in my tables, if they were prepared for the purpose" (Galton, 1869, p. 370). The law of ancestral heredity, he recognizes, is only a first step toward such a future, but it is one that would be taken up with gusto by Karl Pearson and W.F.R. Weldon, to whom we now turn.

For the biometricians, then, what I think we see are two different ways in which to fill in the details of a Darwinian, gradualist approach to evolutionary theorizing. On the

[22] As noted above, Galton is somewhat of two minds about the question of saltationism versus gradualism, but he nonetheless expresses numerous clear commitments to the idea, even if it is often difficult to see how he puts them into practice.

one hand, Pearson is concerned first and foremost with measurement and prediction, as Galton had been. We thus separate regression from reversion, Pearson argues, because we need to ensure that we are applying the most perspicuous mathematical-predictive tool to the system at hand. These will differ, in the absence of a proper synthesis of Mendelism and biometry, in the cases of alternative and blending inheritance – Weldon's efforts at making the former a special case of the latter are, at this point, far clunkier than simply analyzing alternative inheritance separately.

Weldon, on the contrary, believes that clunkiness is worth the effort, because it would give us precisely the kind of knowledge for which he had been searching: the kind of rich, multi-layered causal analysis that could help us understand why it is that statistical distributions of the relevant sorts appear in the first place. Such a theory would, by an analogy that Weldon often drew, put future biologists in the same position as physicists, who are so confident in the accuracy and scope of their theoretical and observational apparatus that Lord Rayleigh could discover argon as a tiny mathematical remainder left after comparing two chemical reactions (Weldon, 1906, pp. 89–93).

All four of these authors, then, had their own reasons for being attracted to some combination of a set of broad characters that they believed any acceptable theory of evolution should exemplify: uniformitarianism, gradualism, statistical theorizing, and the search for the causes of variation. But as those conceptual commitments were refined, they led each of the four to disagree quite strongly in the details. In short, reversion became an issue for them precisely because it was made salient by these broader desiderata for evolutionary theorizing. Not only are these differing sets of commitments, therefore, interesting in their own right, but they prove crucial for understanding just what it was that made reversion so important to each.

For Fisher, on the other hand, things are more complicated (in this, as in many other ways; see Hodge, 1992). Perhaps most importantly, we can point to his understanding of indeterministic causation and hypothetical populations. Parameters like "death rates or expectations of life" are not properties of actual, real-world populations, but rather of "the hypothetical population sampled, and depend only upon its nature and circumstances" (Fisher, 1930, p. 23). Inferring features of biological populations is thus just like the inference of the parameters of statistical populations from observed samples.

As Margaret Morrison has noted (2002), this constitutes a significant conceptual innovation, which formed part of Fisher's ability to move past Pearson and Weldon's failure to construct a formalized theory of natural selection. Rather than focusing on actual populations of real-world individuals, moving to hypothetical populations, infinite gene pools, and similar processes of idealization gave Fisher the kind of inferential basis he needed to build a generalizable picture of selection's action. In the process, the fact that one particular organism may have reverted to the characters of an ancestor simply stops being a pertinent biological phenomenon – such an individual can of course be located somewhere within our hypothetical population, but the tracking or explaining of individual outcomes, and hence of reversions, is just no longer a relevant part of Fisher's evolutionary worldview. The way in which Fisher wants to build a populational, statistical biology leaves no room for reversion as a problem to be solved.

4. The Demise of Scientific Problems

While assigning historical causation is never a knockdown matter, I think the brief sketches I have offered here constitute strong evidence that the most powerful explanation for the rise and fall of reversion is in fact a shift in these sorts of conceptual features of evolutionary theorizing, as Darwin's non-mathematical, gradualist, uniformitarian understanding of the nature of scientific theorizing was adapted and formalized by the biometricians, until by Fisher's day it had been abstracted to such an extent that the phenomena of reversion ceased to be evoutionarily germane. The extraordinary rapidity of reversion's ascent and descent, then, simply parallels the extraordinary rate of change that we saw throughout the evolutionary sciences in this period, as we move from an essentially non-mathematical, non-chancy theory of evolution in Darwin's notebooks of the 1830s to that of the early Modern Synthesis, for which statistics has become an essential tool.

I want to conclude, finally, by generalizing from this example and leaving the particular case of reversion behind. Might we be able to say something more about the death of scientific problems in general? What makes a scientific problem cease to be interesting? As I've used it here, this amounts to asking: why would something that was once taken to be a crucial phenomenon to be explained, a problem in the sense of being a *problematic* case, cease entirely to be viewed in such a way?

There is some precedent for a general discussion of this question. Kuhn, for instance, considered what, in his approach to the nature of scientific inquiry, he called the resolution of anomalies. As he put the matter in *Structure of Scientific Revolutions*, there are exactly three ways in which an anomaly might end – by being assimilated back into the tradition of normal science, by being set aside, or by triggering a scientific revolution (Kuhn, 1996, p. 84). More illuminatingly, he unpacked such changes in more detail in a lecture which predates *Structure*. There, he described three ways in which an anomaly might fail to rise to the level of a crisis – by being revealed to be an instrumental effect, by ceasing to exist on replication, or by being set aside for future researchers (Kuhn, 1961, p. 178) – and four ways in which a crisis might in turn be resolved – by yielding to new experimental or theoretical resources developed broadly in the context of current theory, by being left open despite widespread recognition of crisis status, by the discovery of a genuinely novel phenomenon, or by the development of genuinely novel theory (Kuhn, 1961, p. 179).

While such a categorization is helpful, Kuhn's focus on anomalies here means that it is difficult for us to see how we might extrapolate from his understanding of these shifts to the abandoning of scientific problems that occurs during the process of normal science.[23] More useful, then, is Laudan's approach to scientific change in terms of scientific problems. Reversion, for example, constitutes a classic instance of an *empirical problem*, or, in Laudan's terms, "anything about the natural world which strikes us as odd, or otherwise in need of explanation" (Laudan, 1978, p. 15). Solving emprical

[23]In addition to being important to a general theory of problem change, for the case of reversion in particular, and despite the frequent depiction of this period as shaped by the unfolding crisis between biometrical and Mendelian views of evolution, I have argued elsewhere that this period is in fact better understood as proceeding largely incrementally (Pence, 2022).

problems is the primary business of science, for Laudan, and "an empirical problem is solved when, within a particular context of inquiry, scientists properly no longer regard it as an unanswered question" (Laudan, 1978, p. 22).

Laudan notes, however, that problems move from non-problem, to unsolved problem, to solved problem, and back, regularly as science develops. This movement, then, is perhaps less important for our purposes here than the idea of *problem weighting* – for it is not just the solution of problems that matters, but the solution of important problems. Problems can gain importance, for example, by being empirically solved (for there are always many potential problems that lack solutions), by being anomalous (that is, in what we might call a "comparative" version of Kuhn's original notion of anomaly, by being solved by one theory but not by its competitors), by becoming the archetype of an entire class of solutions, or by being more generally stated (Laudan, 1978, pp. 33–35). Conversely, less important problems might be those that have been conceptually dissolved (i.e., shown to be a non-problem), moved out of the domain of a given science, or ceased to function as an archetype (Laudan, 1978, p. 36).

The most valuable approach to this question, then, might be to imagine "being a scientific problem" as a matter of degree rather than a matter of kind. (It is already, as Laudan notes, a matter of context, as of course problems are only problems for a particular theory, given a particular evidence base, for particular scholars, at a particular time.) What matters, then, is the relative importance of such problems. A particular way of expressing a problem therefore has a kind of dynamics, as we watch its importance wax and wane over the course of its life.

In that sense, we can readily tally the factors highlighted both by Kuhn and by Laudan as features that matter for the dynamics of problem importance. Empirical resolution, whether of the trivial (ceasing to be apparent after replication) or the profound (yielding to a novel experimental technique) sort, is obviously a major force. New theoretical resources are another. The realization that a problem is anomalous is perhaps the most important contextual or social factor in those dynamics (along with other features of institutional or publishing prestige). Ethical and social values could also effect change in importance; a problem might become unimportant because we come to disvalue the kind of research, results, or side effects that a problem engenders.[24] We can even recover something of Kuhn's sense of revolution here, by noting that radical revisions in response to a problem – like dubbing it a new scientific phenomenon, or developing a radically new theory to encompass it – will indeed change the problem's importance, but by changing the underlying context, and hence will change the importance of other problems in interrelated and perhaps unpredictable ways. On this view, however, it is a category mistake to say, as Kuhn does, that the "relevance" of a problem is yet another force governing those dynamics. Irrelevance simply *is* low problem-importance, and a problem's being set aside for future researchers is a reasonable reaction to such low problem-importance.

To close, return to the way in which, as I've argued, Fisher's instantiation of a commitment to statistical, populational evolutionary theory made the phenomenon of

[24] Think, here, of cases like eugenics or vivisection; my thanks to John Dupré for bringing up the possibility.

reversion cease to be relevant. Reversion did not therefore become a *solved* question for Fisher – rather, it slid far down the importance scale as a result of the ontology which he constructed for understanding evolution. Much like the question of how many blades of grass are found in my garden, while it remains a question ostensibly about biological phenomena, it is simply one that no longer features in important scientific explanations. Analyzing the dynamics of such changes in scientific importance, I think, can offer us an interesting and revealing way to think about the development of scientific disciplines.

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