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Author(s): P. Kyle Stanford
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P. Kyle Stanford

ABSTRACT

In earlier work I have argued that the most substantial threat to scientific realism arises from the problem of unconceived alternatives: the repeated failure of past scientists and scientific communities to conceive of alternatives to extant scientific theories, even when such alternatives were both (1) well confirmed by the evidence available at the time and (2) sufficiently scientifically serious as to be later embraced by actual scientific communities. In this paper I explore Charles Darwin's development and defense of his 'pangenesis' theory of inheritance and conclude that this particular historical example offers impressive support for the challenge posed to realism by this problem of unconceived alternatives.

1 Introduction

Scientific realists hold that our best scientific theories are successful because the descriptions they offer of otherwise inaccessible domains of nature are at least probably and/or approximately true. Opponents of this commonsensical view have typically grounded their challenges either in arguments from the underdetermination of theories by the available evidence, or in the 'pessimistic induction' from the falsity of many past successful theories to the likely

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falsity of our own. In recent and forthcoming work ([2001], [2006]), I have argued that the traditional arguments in support of underdetermination and the pessimistic induction leave much to be desired. The argument for underdetermination from empirical equivalents succeeds only where it trades in any distinctive concern about theoretical science for general skeptical worries that apply equally well to any knowledge claim whatsoever, while the pessimistic induction ignores important differences between the degrees or varieties of success enjoyed by past theories and those of our own day that might lead us to reasonably resist the inductive projection from past to present cases. But I also argue that scientific realism faces a much more serious threat from a very different sort of historical pattern. What should actually give realists pause, I suggest, is our repeated failure *even to conceive of* alternatives to our scientific theories that were nonetheless both well confirmed by the evidence available at the time and sufficiently serious as to be ultimately accepted by some actual scientific community in the course of further inquiry.

Why does this problem of unconceived alternatives pose any serious threat to scientific realism? In typical cases, the justification we offer for believing a fundamental theory about the entities and dynamical principles at work in some otherwise inaccessible domain of nature is abductive or eliminative in character: we arrive at a decision to believe or accept a given theory because we think it offers the best available explanation for the empirical evidence we have and because we regard rival or competing explanations of that same evidence as convincingly eliminated or discredited. But as Duhem eloquently noted long ago, such an abductive or eliminative inferential procedure will only guide us to the truth about nature if the truth is among the competing explanations or hypotheses we are considering in the first place:

> Between two contradictory theorems of geometry there is no room for a third judgment; if one is false, the other is necessarily true. Do two hypotheses in physics ever constitute such a strict dilemma? Shall we ever dare to assert that no other hypothesis is imaginable? Light may be a swarm of projectiles, or it may be a vibratory motion whose waves are propagated in a medium; is it forbidden to be anything else at all? ([1954], pp. 189–90)

What seems to have worried Duhem is the possibility that there might be equally well confirmed alternative hypotheses about the nature of light that we simply have not conceived of in the first place. Unconceived alternatives of this sort would indeed threaten the eliminative or abductive support we can offer for even the best of our own scientific theories, and I have suggested elsewhere that the historical record of scientific inquiry itself is the best source of evidence we have to use in deciding whether this is a serious challenge rather than a mere speculative possibility. Of course, a competing theory need not accommodate all of the evidence available at a given time to count as well confirmed, nor need we deny that an older theory can sometimes explain phenomena that a successor cannot or cannot immediately: two theories may simply have *different* explanatory accomplishments and *different* evidential anomalies while both remaining reasonably well confirmed by the totality of the evidence available at a given time. Nonetheless, if the historical evidence confirms that past practitioners have indeed routinely failed to conceive of well-confirmed alternative hypotheses of this sort that were sufficiently serious as to be actually accepted by later scientific communities, then we have every reason to believe that there are similar alternatives to our own contemporary scientific theories that remain *presently* unconceived, even if we cannot specify or describe them further. This challenge to scientific realism enjoys several advantages over the traditional pessimistic induction, but perhaps the most important is that the problem of unconceived alternatives concerns the *theorists* rather than the *theories* of past science: even if contemporary scientific theories sometimes enjoy empirical successes arguably unprecedented in their scope and character, this offers us no reason to suppose that today's scientists are any better at conceiving of the full range of theoretical possibilities confirmed by this evidence than were the greatest scientific minds of the past.

I have offered ([2001], p. S9, [2006], Ch. 1) a list of examples of important historical successions of scientific theories that seem to exemplify this problem of unconceived alternatives, but any convincing case for the importance of the challenge will clearly have to stand or fall with a close analysis of the details of the historical record in these cases. In this paper, I will make a start on this work by examining just one such example in the requisite detail: Charles Darwin's development and defense of his 'pangenesis' theory of inheritance. My claim is that the details of this development and defense clearly demonstrate Darwin's failure to conceive of scientifically serious alternative theoretical possibilities that were nonetheless equally well-confirmed by the evidence available to him, and thus support my earlier contention that the problem of unconceived alternatives poses a clear and present danger to scientific realism.

I choose this example in part because we might expect any positive evidence of the problem we can find in this particular case to be especially revealing. For one thing, the staunch tradition of realism among both scientists and philosophers in the life sciences might naturally suggest that evidence of our historical vulnerability to the problem should be particularly difficult to come by in this arena. Furthermore, Darwin's theorizing about inheritance is at least broadly continuous with our own: pangenesis was first presented publicly in 1868, at a time when at least some influential theories of growth, development, and inheritance (traditionally regarded as aspects of the single subject of 'generation') had begun to be directed towards roughly the same collection of phenomena and to be articulated under roughly the same broad metaphysical constraints as today's theories of genetics and embryology. But perhaps most important of all, the most consequential alternative line of later theorizing about inheritance that remained unconceived by Darwin did not, as we shall see, require the development of radically new scientific concepts (by contrast with, say, the inception of quantum mechanics). And needless to say, the existence of scientifically serious and well-confirmed unconceived alternatives *that required no radical conceptual innovation* would seem to argue especially strongly for the general significance of the problem.

2 Darwin and pangenesis: The search for the material basis of generation and heredity

From the middle to the end of the 19th century, interest in identifying some material basis for the transmission of characteristics from parents to offspring gained dramatic momentum from such converging influences as increasingly detailed microscopic observations, the development of cell theory, and advances in experimental hybridization. But each of these developments was in turn prompted at least in part by the publication (in 1859) of Charles Darwin's *Origin of Species* and the importance thereby conferred on questions about the mechanism of evolution and, consequently, about the sources of variation in nature (see Dunn [1965], p. 34; Gasking [1967], p. 161; Geison [1969], pp. 375, 385–6; Robinson [1979], pp. xiii, 3; Cowan [1985], Ch. 5; Olby [1985], Ch. 3; Bowler [1989], p. 46; Gayon [1998], Ch. 1).[2] Though various kinds of hereditary particles had been proposed by Buffon, Diderot, Maupertuis and others in the period before Darwin, the idea of living or material units or particles[3] as the substrate of inheritance that is developmentally continuous with our own is usually traced back to the 'physiological units' introduced by Herbert Spencer in his *Principles of Biology* ([1864]) and

2 Note that here and throughout I have tried to restrict my use of the secondary literature concerning this period in the history of science to classic discussions whose central contentions still appear to be widely accepted, rather than to the unavoidably more contentious claims embodied in more recent historical scholarship. As will become clear in what follows, however, the direct evidence I adduce in support of the problem of unconceived alternatives is drawn almost exclusively from primary sources, rather than from this secondary literature. Of course, if more recent developments in the historical scholarship concerning this period undermine either my reading of the primary sources or the use I have made of them in trying to establish the general significance of the problem itself, I trust that my colleagues in the history of science will set me straight.

3 A terminological caution: the term 'particulate' heredity is often used to describe views on which specific *characteristics* or the material foundations for them are inherited in a discrete fashion, that is, in opposition to 'blending' heredity (in which parental characteristics or their material causes are mixed or amalgamated in the offspring). While views like Darwin's and Spencer's certainly involved the postulation of material particles inherited by offspring from parents, they were not particulate views of heredity in this important sense.

to the 'gemmules' of Darwin's own theory of pangenesis, first proposed in his *Variation of Animals and Plants Under Domestication* in 1868 (hereafter *Variation*)[4] Although Spencer's version of this general idea was published 4 years earlier, Darwin's account seems not to have been based on it in any way,[5] having been by that time under construction for some 20-odd years.[6] In any case, it was Darwin's more concrete and more clearly mechanistic hypothesis of pangenesis which would exercise a greater influence on subsequent theorizing about generation and inheritance and which later theorists would feel obliged to confront and discuss, even if only to abuse it (Robinson [1979], Introduction, Ch. 1 (esp. p. 24) and passim; Churchill [1987], p. 343; see also Endersby [2003], p. 81).

Notwithstanding the continuities noted above, Darwin did not share our view of heredity and variation as complementary aspects of a single process; as any number of commentators have pointed out, he instead subscribed without substantial reflection to a longstanding view of these as antagonistic forces or principles operating in opposition to one another (e.g. Churchill [1987], pp. 343–5; Bowler [1989], pp. 25, 68; Hodge [1989], p. 277; see also Gayon [1998], Ch. 1; for an especially clear expression from Darwin himself, see [1905], v. ii, p. 453). Darwin thus came to suggest that variations between parents and offspring were anomalous incidents, produced largely if not exclusively by changes or irregularities in the 'conditions of life' and taking place against a broad background of inherited characteristics: he suggests

[4] Except where otherwise noted page numbers will refer to the 1905 republication of the second edition of this work as a 'popular edition' by the original publisher, John Murray.

[5] See Darwin to Hooker, February 23 {1868} in *Life and Letters of Charles Darwin* ([1959], v. ii, pp. 259–61; and Darwin to Wallace, February 27 {1868} in [1959], v. ii, p. 262). As a general matter, the similarities between Darwin's account and any number of earlier views of inheritance appealing to material units or particles seem to have caught him somewhat by surprise (see letters from Darwin to Huxley, July 12 {1865?} in [1959], v. ii, p. 228; Darwin to Huxley, {1865?} in [1959], v. ii, pp. 228–9; and Darwin to Ogle, March 6 {1868} in [1959], v. ii, p. 265): the pangenesis manuscript of 1865 contained no mention of related earlier theories, the first edition of *Variation* discussed those of Buffon, Bonnet, Spencer, and Owen, and the second edition added mention of more views 'nearly similar' to pangenesis by Hippocrates, Ray, and a Prof. Mantegazza ([1905], v. ii, p. 457n; see Geison [1969], p. 393). Of course, the fact that the *general* suggestion of hereditary particles thrown off by parts of the body had been previously made should not lead us to think that pangenesis itself was not really new or was not genuinely unconceived before Darwin's work in the mid-19th Century: as Geison notes, 'Darwin could probably have demonstrated... fundamental differences between his ideas and those of any of the pre-19th century pangenetic theorists' ([1969], p. 395).

[6] In August of 1867 Darwin wrote to Charles Lyell 'I do not know whether you have ever had the feeling of having thought so much over a subject that you had lost all power of judging it. This is my case with Pangenesis (which is 26 or 27 years old)...' (Darwin to Lyell, August 22 {1867} in [1959], v. ii, p. 255). Further compelling evidence that Darwin was a 'lifelong generation theorist' is provided by Hodge ([1985]; discussed in Bowler [1989], p. 58; see also Endersby [2003]; cf. Geison [1969]). Darwin was also not influenced, of course, by Mendel's reports of his breeding experiments, published in 1866, which lay largely unknown and unappreciated in libraries across Europe, including those of the Royal Society and the Linnean Society in Great Britain (see Olby [1985], p. 103).

that 'we may on the whole conclude that inheritance is the rule, and non-inheritance the anomaly' ([1905], v. ii, p. 454) and that the 'proper function' of reproductive systems is 'transmitting truly the characters of the parents to the offspring' ([1905], v. ii, p. 453). Against this theoretical background, here is Darwin's own description of pangenesis as it appeared in the second (1874) edition of the *Variation*:

> It is universally admitted that the cells or units of the body increase by self-division or proliferation, retaining the same nature, and that they ultimately become converted into the various tissues and substances of the body. But besides this means of increase I assume that the units throw off minute granules which are dispersed throughout the whole system; that these, when supplied with proper nutriment, multiply by self-division, and are ultimately developed into units like those from which they were originally derived. These granules may be called gemmules. They are collected from all parts of the system to constitute the sexual elements, and their development in the next generation forms a new being; but they are likewise capable of transmission in a dormant state to future generations and may then be developed. Their development depends on their union with other partially developed or nascent cells which precede them in the regular course of growth... Gemmules are supposed to be thrown off by every unit, not only during the adult state, but during each stage of development of every organism; but not necessarily during the continued existence of the same unit. Lastly, I assume that the gemmules in their dormant state have a mutual affinity for each other, leading to their aggregation into buds or into the sexual elements. Hence, it is not the reproductive organs or buds which generate new organisms, but the units of which each individual is composed. These assumptions constitute the provisional hypothesis which I have called Pangenesis. ([1905], v. ii, p. 457)

Darwin writes that it is the evident relation between 'large classes of facts, such as those bearing on bud variation, the various forms of inheritance, the causes and laws of variation' and 'the several modes of reproduction' which have 'led, or rather forced' him to form a view connecting them ([1905], v. ii, p. 432). And he offers a characteristically exhaustive list of phenomena for which he suggests pangenesis alone can account:

> How it is possible for a character possessed by some remote ancestor suddenly to reappear in the offspring; how the effects of increased or decreased use of a limb can be transmitted to the child; how the male sexual element can act not solely on the ovules, but occasionally on the mother-form [under this heading Darwin also later includes its effect on the offspring of later matings]; how a hybrid can be produced by the union of the cellular tissue of two plants independently of the organs of generation; how a limb can be reproduced on the exact line of amputation, with neither too much nor too little added; how the same organism may be produced by such widely different processes, as budding and true seminal generation; and lastly, how of two allied forms, one passes in the course of

> its development through the most complex metamorphoses, and the other does not do so, though when mature both are alike in every detail of structure. ([1905], v. ii, pp. 432–3).

As Darwin saw it, the central idea capable of explaining each of these disparate phenomena and of unifying them all was that 'an organism does not generate its kind as a whole but each separate unit generates its kind' ([1905], v. ii, p. 490). More fully, 'every separate part of the whole organization reproduces itself. So that ovules, spermatozoa, and pollen-grains,—the fertilized egg or seed, as well as buds,—include and consist of a multitude of germs thrown off from each separate part or unit' ([1905], v. ii, p. 433). He grants that this is 'merely a provisional hypothesis or speculation' which might involve incompleteness or error, but insists nonetheless that 'until a better one be advanced, it will serve to bring together a multitude of facts which are at present left disconnected by any efficient cause' ([1905], v. ii, p. 433).

An important source of Darwin's insistence that these phenomena of generation and inheritance had yet to be connected by 'any efficient cause' and that pangenesis alone provided an explanation of them was his refusal to regard appeals to vitalistic powers or potentials as offering any genuine explanatory *alternative* to pangenesis at all. He argues that such talk of potentialities and powers should itself be understood *in terms of* the central theoretical mechanism postulated by pangenesis: 'It has often been said by naturalists that each cell of a plant has the potential capacity of reproducing the whole plant; but it has this power only in virtue of containing gemmules derived from every part' ([1905], v. ii, p. 490). Similar sentiments appear in the Author's Preface (dated March 28, 1868) to the first American edition of the *Variation*: 'I venture to call the reader's attention to the chapter on Pangenesis. The view there propounded is simply hypothetical, but it has appeared to me...to be no small gain to seize on a material bond, by which the various forms of reproduction inheritance, development, etc. can be connected together. We thus get rid of such vague terms as spermatic force, the vivification of the ovule, sexual potentiality, and the diffusion of mysterious essences or properties from either parent, or from both, to the child.' But Darwin's insistence that vitalistic appeals to powers or potentials offered no genuine explanatory competitor to pangenesis is perhaps most eloquently expressed in a letter to Hooker written just a month after the publication of the *Variation* in 1868:

> When you [Hooker] or Huxley say that a single cell of a plant, or the stump of an amputated limb, have the 'potentiality' of reproducing the whole—or 'diffuse an influence,' these words give me no positive idea; —but when it is said that the cells of a plant, or stump, include atoms derived from every other cell of the whole organism and capable of development, I gain a distinct idea. But this idea would not be worth a rush, if it applied to one

> case alone; but it seems to me to apply to all the forms of reproduction—inheritance—metamorphosis—to the abnormal transposition of organs—to the direct action of the male element on the mother plant, &c. Therefore I fully believe that each cell does *actually* throw off an atom or gemmule of its contents; —but whether or not, this hypothesis serves as a useful connecting link for various grand classes of physiological facts, which at present stand absolutely isolated (Darwin to Hooker, February 28 {1868} in [1959], v. ii, p. 264).[7]

Besides illustrating his reasons for thinking that vitalistic appeals offered at best an intolerably vague description of the sort of mechanism posited by pangenesis itself, this letter also clearly reflects Darwin's insistence that his hypothesis *alone* offers a 'positive' or 'distinct' idea capable of explaining and unifying a wide variety of the phenomena of heredity and generation 'which at present stand absolutely isolated'. Furthermore, Darwin here reports that this fact was sufficient to lead him to 'fully believe' in the literal truth of at least the theory's central claim that each cell does indeed throw off gemmules.

But how can we know that Darwin really failed to conceive of possible mechanistic alternatives to pangenesis at all, rather than, say, finding sufficient fault to simply dismiss them out of hand as unacceptable, as he seems to have treated Hooker's conception of vitalistic powers? While some later theorists of inheritance would argue that particular aspects of their own theories were either necessary features of any hypothesis of physiological units of inheritance (e.g., Galton), or forced on us by the empirical phenomena themselves (e.g., Weismann), Darwin never suggests that the phenomena of inheritance, growth, development, reproduction and repair could not *possibly* be otherwise explained. Instead he offers explicit and repeated assurances (even in the title of the chapter in which it is offered) that his hypothesis is 'provisional' and tentative, apparently in response to what seems to have been a skeptical reaction by Huxley to the pangenesis manuscript of 1865 (see Olby [1963]; Robinson [1979], p. 16).

Nonetheless, despite this characteristic caution with which Darwin presented to the world the theory he told Gray 'will be called a mad dream' (October 16 {1867} in [1959], v. ii, p. 256), his private correspondence offers convincing evidence that he really did fail to conceive of relevant alternatives: besides remarking (in the passages noted above) that the known phenomena of heredity and generation are 'absolutely isolated' and 'disconnected by any efficient cause,' Darwin repeatedly *tells* his correspondents that pangenesis

[7] Darwin quite frequently neglected to include the year on the dates of the letters he wrote. In these cases, when the year of a letter's date is not recorded on the letter itself and has instead been inferred from content or context, this is indicated in the text using the following style, e.g., {1865}, rather than the more traditional square brackets, e.g. [1865], for ease of legibility.

is the first and only theory he has conceived of that can account for them. In asking Huxley to review his manuscript of the proposed chapter on pangenesis in the first place he writes as follows:

> ...in my next book [1905] I shall publish long chapters on bud- and seminal-variation, on inheritance, reversion, effects of use and disuse, &c. I have also for many years speculated on the different forms of reproduction. Hence it has come to be a passion with me to try to connect all such facts by some sort of hypothesis. The MS. which I wish to send you gives such a hypothesis; it is a very rash and crude hypothesis, yet it has been a considerable relief to my mind, and I can hang on it a good many groups of facts. (Darwin to Huxley, May 27 {1865?} in [1959], v. ii, pp. 227–8)

He writes to Hooker that 'though I can see how fearfully imperfect, even in mere conjectural conclusions, it is; yet it has been an infinite satisfaction to me somehow to connect the various large groups of facts, which I have long considered, by an intelligible thread' (Darwin to Hooker, November 17 {1867} in [1959], v. ii, p. 257). He takes himself to echo Wallace's own feelings in saying 'that it is a relief to have some feasible explanation of the various facts, which can be given up as soon as any better hypothesis is found. It is certainly an immense relief to my mind; for I have been stumbling over the subject for years, dimly seeing that some relation existed between the various classes of facts' (Darwin to Wallace, February 27 {1868} in [1959], v. ii, p. 262; and in [1903], v. i, p. 301). To Hooker he quotes Wallace[8] as saying 'It is a *positive comfort* to me to have any feasible explanation of a difficulty that has always been haunting me, and I shall never be able to give it up till a better one supplies its place, and that I think hardly possible, &c.', adding that Wallace's words 'express my sentiments exactly and fully: though perhaps I feel the relief extra strongly from having during many years vainly attempted to form some hypothesis' (Darwin to Hooker, February 28 {1868} in [1959], v. ii, p. 264, original emphasis). He tells G. Bentham that 'to my mind the idea has been an immense relief, as I could not endure to keep so many large classes of facts all floating loose in my mind without some thread of connection to tie them together in a tangible method' (Darwin to G. Bentham, April 22 {1868} in [1903], v. ii, p. 371). He writes to Fritz Müller 'I find it a great relief to have some definite, though hypothetical view, when I reflect on the wonderful transformations of animals, the regrowth of parts, and especially the direct action of pollen on the mother-form, &c.' (Darwin to Müller, June 3 {1868} in [1903], v. ii, p. 82). Thus we seem faced with a wealth of occasions on which Darwin simply *reported* that pangenesis was the only hypothesis he knew of or could conceive of that would explain the diverse phenomena of generation and inheritance demanding his attention. If Darwin did consider

[8] From a letter written to Darwin himself (February 1868 in [1903], v. i, p. 300).

alternative possibilities or proposals for a mechanistic account of heredity and generation, he worked hard to keep us from knowing about them, for (in stark contrast to his treatment of vitalistic powers) none of these various reflections, assurances, or confessions show any evidence of entertaining and dismissing such alternatives; instead he repeatedly insists that pangenesis is the lone serious contender.[9]

Given Darwin's apparent inability to conceive of any alternative to pangenesis' fundamental strategy for explaining the phenomena of heredity and generation, perhaps it is unsurprising that in his private correspondence Darwin was much less circumspect about the theory's prospects and much more confident that his 'beloved child' (Darwin to Hooker, February 3 {1868} in [1959], v. ii, p. 258), 'an infant cherished by few as yet, except his tender parent, but which will live a long life' (Darwin to Gray, May 8 {1868} in [1959], v. ii, p. 266), would ultimately win the day. To Huxley he writes that he is 'becoming convinced that some such view will have to be adopted' (Darwin to Huxley, May 30 {1865} in Darwin [2002]), to Gray that he thinks it 'contains a great truth' (Darwin to Gray, October 16 {1867} in [1959], v. ii, p. 256), to F. Hildebrand that he believes it 'will ultimately be accepted' (Darwin to Hildebrand, January 5 {1868} in [1903], v. i, p. 285) and to Müller that 'Pangenesis will turn out true someday!' (Darwin to Müller, May 12 {1870} in [1903], v. ii, p. 359). To William Ogle he writes, 'I advance the views merely as a provisional hypothesis, but with the secret expectation that sooner or later some such view will have to be admitted' (Darwin to Ogle, March 6 {1868} in [1959], v. ii, p. 265) and to J. J. Weir that 'I fully believe pangenesis will have its successful day' (Darwin to Weir, March 17 {1870} in [1903], v. i, p. 320). In an unpublished letter of July 14, 1868, Darwin advises Hooker not to touch on pangenesis in an upcoming address in light of the many luminary figures opposed to the theory, but nonetheless reports that 'my conviction is unshaken that it will hereafter be looked at as the best hypothesis of generation, inheritance [and] development.' And a later unpublished letter to J. V. Carus offers the similar view that 'after mature reflection I believe that physiologists will some day be compelled to admit some such doctrine' (October 19, 1868).[10]

Moreover, Darwin explicitly links his confidence that pangenesis will triumph or reappear with his inability to identify any alternative

[9] I defer for the moment discussing the possibility that *given the phenomena he took to exist*, Darwin was *right* to think that (some version of) pangenesis alone could offer a convincing explanation for them.

[10] My sincere thanks to the Cambridge University Library for providing me a reproduction of Darwin's unpublished letter to Hooker, and to the Staatsbibliothek zu Berlin—Preußischer Kulturbesitz for providing me with a reproduction of Darwin's unpublished letter to Carus (Slg. Darmst. Lc 1859 (9): Darwin, Charles Robert—Brief vom 19.10 {1868} an Victor Carus [=Br. Nr. 14]).

explanation for what he considered the central phenomena of heredity. After receiving Huxley's apparently sharp criticism of the pangenesis manuscript of 1865 he writes, 'I do not doubt your judgment is perfectly just, and I will try to persuade myself not to publish. The whole affair is much too speculative; yet I think some such view will have to be adopted, when I call to mind such facts as the inherited effects of use and disuse, &c.' (Darwin to Huxley, July 12 {1865?} in [1959], v. ii, p. 228). And to Hooker, Darwin again grounds his confidence that pangenesis will reappear in his inability to conceive of any alternative explanation for the wide variety of hereditary phenomena for which he thinks pangenesis alone accounts:

> You will think me very self-sufficient, when I declare that I feel *sure* if Pangenesis is now stillborn it will, thank God, at some future time reappear, begotten by some other father, and christened by some other name.
>
> Have you ever met with any tangible and clear view of what takes place in generation, whether by seeds or buds, or how a long-lost character can possibly reappear; or how the male element can possibly affect the mother plant, or the mother animal, so that her future progeny are affected? Now all these points and many others are connected together, whether truely or falsely is another question,[11] by Pangenesis. (Darwin to Hooker, February 23 {1868} in [1959], v. ii, p. 261, original emphasis).

As late as 1873 Darwin confessed to De Candolle that '[a]lthough my hypothesis of pangenesis has been reviled on all sides, yet I must still look at generation under this point of view...' (Darwin to De Candolle, January 18 {1873} in [1903], v. i, p. 348). It seems hard to understand this intransigence, not to mention Darwin's repeated assurance that pangenesis would ultimately be embraced, unless we assume that its source lies in what Darwin elsewhere frankly admits: that he could conceive of no other mechanistic hypothesis able to account for what he regarded as the central phenomena of generation and inheritance.

3 A crucial unconceived alternative: common-cause mechanisms of inheritance

Eschewing the benefits of scientific hindsight, it is easy to sympathize with Darwin's sense that pangenesis (or some close relative) represented the only *possible* mechanical explanation of the phenomena of generation and

[11] This reservation is somewhat surprising, for in another letter to Hooker just 5 days later Darwin would write that pangenesis' singular explanatory achievements lead him to 'fully believe that each cell does *actually* throw off an atom or gemmule of its contents' (Feb. 28 {1868} in [1959], v. ii, p. 264; see above).

inheritance that interested him: after all, how could features of offspring so accurately reflect so many diverse peculiarities of their parents (no matter which of several different methods of reproduction gave rise to them) unless each of the parent's tissues, organs, and other physical features causally contributes to or otherwise serves as a physical template for the formation of the corresponding part of the bodies of its several offspring? Little wonder, then, that Darwin wrote to Müller that 'It often appears to me almost certain that the characters of the parents are "photographed" on the child, only by means of material atoms derived from each cell in both parents, and developed in the child' (Darwin to Müller, June 3 {1868} in [1903], v. ii, p. 82).

But once the question and answer are phrased in this way it is quite easy, in retrospect, to articulate at least one broad class of serious theoretical alternative possibilities that seems to have escaped Darwin's consideration completely: *parents and offspring might share salient characteristics not because the parents' tissues or other physical features themselves contribute materially or even causally to the formation of those of the offspring but instead because both sets of tissues, organs and features (with their shared peculiarities) are produced by shared germinal materials, of which identical or systematically related versions are invariably passed from parents to offspring*. That is, the tissues of the offspring (produced by whatever intervening mechanism) might recapitulate salient features of the parent's *not* because the latter serve as causes of the former, but because they share a *common-cause* in the hereditary materials found in a shared germ line ultimately producing them both.

Note that this suggestion does not require us to Whiggishly dismiss the full range of phenomena Darwin invoked pangenesis to explain and focus instead on just those unified and accounted for by contemporary genetics: this is because the explanatory promise held out by pangenesis for the phenomena of heredity and generation holding Darwin's interest *survives* a shift from pangenesis' conception of hereditary particles as links in a causal chain (leading from the traits and developed tissues of the parent to those of the offspring) to the alternative idea of a shared germinal source of such particles serving as a common-cause of traits and tissues in both parent and offspring. That is to say, Darwin's pangenetical explanations ([1905], v. ii, pp. 467–88) of reversion, of bud-variation, of graft-hybrids, of parthenogenesis, of the development of complex tissues, of the processes of repair (and their precision), of the continuity between various forms of reproduction, of the possibility of producing identical organisms by both budding and seminal generation and with or without complex metamorphoses, and even of phenomena whose existence Darwin accepted but which we deny, like the direct influence of the 'male sexual element' on the tissues of the mother plant (later called xenia or metaxenia) and on later progeny of the same female animal by different males (telegony),[12] all *remain available to us* if we allow that the processes of generation, inheritance, growth, development, and repair are mediated by hereditary particles distributed throughout the body but suppose that the source of such particles is a continuous germ line that can be passed in a variety of ways from parent to offspring rather than the developed tissues of the parent organism itself.

Perhaps most importantly of all, the proposal would not have required Darwin to give up his famous commitment (especially late in life) to the inheritance of acquired characters,[13] because we need not suppose the germ line to be *isolated* in order to have the fundamental mechanical structure that Darwin fails to consider. We might suppose, for instance, that the germinal materials passed on to the offspring can themselves be affected by 'mutilations and... accidents, especially or perhaps exclusively when followed by disease.... the evil effects of the long-continued exposure of the parent to injurious conditions.... the effects of the use and disuse of parts, and of mental habits' and '[p]eriodical habits' ([1905], v. ii, pp. 70–1) without thereby giving up the idea that shared peculiarities of parent and child are *generally* effects of a common-cause rather than links in a causal chain. That is, we might simply accept that the conditions in which the inheritance of acquired characters was supposed to occur were just those in which activities or events affecting the parent's body can exercise some influence on the shared germinal source of hereditary particles passed on to the offspring: we might even propose (as Francis Galton would later in connection with his own 'common-cause' alternative to pangenesis) a separate, gemmule-mediated

12 Such phenomena actually provide a nice illustration of one specific way in which the original pessimistic induction's willingness to project from past to present science is too simple, for much of the evidence of these phenomena for which Darwin was concerned to account was gathered from famous anecdotes (such as that of Lord Morton's chestnut mare; see [1905], v. ii, p. 446, [1903], v. ii, p. 359), folk wisdom, the stories of animal breeders, and the like (see Olby [1985], pp. 44 and 79, where the mare's owner is given as Lord Moreton), while the concerted efforts of more recent scientific methodology have undoubtedly established more stringent standards for the collection of data. But this difference does not mitigate the problem of unconceived alternatives, as Darwin was unable to exhaust the space of plausible explanations for the phenomena for which *he* thought a theory of generation needed to account.

13 A note of caution is in order here, however. As Winther documents ([2000], pp. 436–9), Darwin felt increasingly forced to make room in his theory for a source of systematic, directed, non-random, or necessarily adaptive variation (including the inheritance of acquired characteristics) by the need to publicly accept Kelvin's estimate of the age of the Earth (which seemed to allow insufficient time for natural selection to produce present organismic diversity from a pool of purely random variation; see also Gayon [1998], pp. 87–8) which he privately rejected. Furthermore, Darwin clearly saw the danger thus posed to the theory of natural selection: as he wrote to Asa Gray in 1868, 'If the right variations occurred, and no others, natural selection would be superfluous' (cited in Winther [2000], p. 439; see also Gayon [1998], p. 54). Thus, while Darwin was certainly convinced (along with many other naturalists of the 19th Century) that the inheritance of acquired characters occurred, it would be easy to overestimate the importance he sincerely ascribed to this mechanism on the basis of the second edition of the *Variation* and other late published writings.

mechanism to account for the inheritance of acquired characters wherever (or *if* ever, as Galton would insist) the phenomenon could be conclusively established. Indeed, this suggestion seems parallel to Darwin's own treatment of distant reversion: he accounts for the possibility by suggesting that gemmules will sometimes lay dormant for generations before developing (often triggered, he suggests, by hybridization or by changes in the 'conditions of life'; [1905], v. ii, pp. 455, 486), but he has very little in the way of a substantive account to offer (see [1905], v. ii, p. 357) of why or the mechanism whereby they do so.[14] Reversion and the inheritance of acquired characters were perhaps the two most important puzzles about heredity for which Darwin hoped to account (see Geison [1969], pp. 388–91, 410; see also Endersby [2003], pp. 78–80), but it would seem to involve no less of an explanatory lacuna to suggest that 'sometimes events during life can affect a shared germinal *source* of characteristics that is passed on to subsequent offspring' than it does to say of distant reversion simply that 'sometimes gemmules can lay dormant for generations before being developed.'

Furthermore, much of Darwin's own explanation of the inheritance of acquired characters can be preserved even on the assumption that shared characteristics of parents and offspring are effects of a common-cause rather than links in a causal chain. The cases of the inheritance of acquired characters that Darwin regarded as most convincing were those in which the mutilation or amputation of a part of the parent was accompanied or followed by disease, rather than simply repeated for generations. His explanation of this difference was that 'all the gemmules of the mutilated or amputated part are gradually attracted to the diseased surface during the reparative process, and are there destroyed by the morbid action' ([1905], v. ii, p. 484). And we can certainly retain this account of the *difference* between mutilations or amputations of diseased versus non-diseased tissues if we suppose that the constant

[14] Darwin seems to recognize this, concluding merely that we have gained 'some insight' ([1905], v. ii, p. 488) into distant reversion and ultimately that '[r]eversion depends on the transmission from the forefather to his descendants of dormant gemmules, which occasionally become developed under certain known or unknown conditions' ([1905], v. ii, p. 491). In the pangenesis manuscript of 1865 he simply attributes distant reversion to 'unknown causes' (Olby [1963], p. 261), and to Hooker he writes that 'crossing races as well as species tends to bring back characters which existed in progenitors hundreds and even thousands of years ago. Why this should be so, God knows' ({September 13, 1864} in [1903], v. ii, pp. 339–40). Nonetheless, the seriousness with which Darwin regarded the demand to explain distant reversion is well illustrated by his reaction to Naudin's account of hybrids as 'living mosaics' without any true fusion of elements from the crossed species: in the margin of his copy of Naudin's prizewinning 1862 essay on hybrids he writes simply 'This view will not account for distant reversion' (Olby [1985], p. 51) and to Hooker he writes that he 'cannot think that [Naudin's view] will hold' giving as his only reason that it 'throws no light, that I can see, on this reversion of long-lost characters' ({September 13, 1864} in [1903], v. ii, pp. 339–40). Nonetheless, Darwin does explicitly follow Naudin's account of reversion in the offspring of ordinary hybrids in ([1905], v. ii, pp. 486–7). On the importance of reversion for Darwin, see also Gayon ([1998], pp. 44–5).

morbid action preferentially depletes gemmules from a shared germinal *source* rather than from a supply already thrown off by the part in question before its amputation. Indeed, Darwin's explanation somewhat implausibly requires that removing the ultimate source of further gemmules (i.e. the amputated tissue or structure) in cases unaccompanied by disease has no effect on their later availability for reproduction, so the suggestion that morbid depletion grounds the difference in hereditary consequences between diseased and undiseased cases seems to fit rather *better* with the idea of a shared germinal source than with a causal chain from parental traits or tissues to those of the offspring in the first place!

Moreover, even if I am wrong to think that Darwin could have simultaneously embraced both the inheritance of acquired characteristics and a common-cause alternative to the structure of inheritance proposed in pangenesis, it would follow only that those cases of the inheritance of acquired characters of which Darwin was confident would have to count as empirical anomalies for any proposed common-cause account of inheritance. But inheriting an anomalous phenomenon of this sort would not automatically disqualify the common-cause hypothesis as a serious contender to pangenesis for explaining the bulk of phenomena that concerned Darwin, for he certainly recognized and tolerated any number of phenomena as anomalies for pangenesis itself: in the *Variation*, for example, Darwin notes that pangenesis cannot explain why gemmules do not spread from bud to bud in plants ([1905], v. ii, p. 462) and that it has no explanation for a number of differences in tendencies to reversion between plants propagated from buds rather than seeds ([1905], v. ii, pp. 480–1). His private correspondence also recognizes empirical anomalies for pangenesis, as when he writes to Hooker that 'even Pan.[genesis] won't explain' the selective impotence of pollen when contacting ovules of same plant (May 21, 1868 in [1903], v. i, p. 302). Similarly, the May 25, 1871 issue of *Nature* published a letter by A. C. Ranyard objecting to pangenesis on the grounds that in graft hybrids, the 'sexual elements produced by the scion' have not been shown to be affected by the stock, annotated in Darwin's copy simply as 'The best objection yet raised' ([1903], v. i, p. 302).

Finally, although belief in the inheritance of acquired characteristics was quite widespread among biologists at the time Darwin wrote (see Cowan [1985], pp. 62–3), its very existence remained a disputed and controversial empirical question even at this time. Perhaps the most influential support for the phenomenon came from famous experiments on guinea-pigs by the physiologist Brown-Séquard (see [1905], v. ii, p. 483; Robinson [1979], p. 22; Cowan [1985], pp. 63–4), but Geison notes that 'opinion was divided among influential 19th Century authors', as James Cowles Prichard, William Lawrence, and Joseph Hooker, for example, seem to have denied that the phenomenon occurred ([1969], p. 379n).[15] Not only was Darwin aware of this resistance to the inheritance of acquired characters, he had rather mild expectations for the ability of his own evidence to change minds, even among his close friends: he writes to Hooker, for instance, that '[w]henever my book on poultry, pigeons, ducks, and rabbits is published, with all the measurements and weighings of bones, I think you will see that 'use and disuse' have at least some effect' ({March} 26 {1862} in [1903], v. i, p. 199). Thus, Darwin could not have failed to recognize that a theory of generation and inheritance would not have needed to allow for the inheritance of acquired characters to constitute a serious contender even in his own day.

What emerges from this lengthy discussion is that Darwin's acceptance of the inheritance of acquired characters certainly posed no insurmountable obstacle and perhaps not even any serious one to recognizing or accepting the possibility of a common-cause structure for inheritance. Such an alternative could have preserved most of the explanatory accomplishments of pangenesis itself, even bettering them in some cases, and the cases of the inheritance of acquired characters Darwin found convincing could either have been reconciled with a common-cause structure for inheritance in a manner analogous to that used for distant reversion or simply left as empirical anomalies for the theory, as he was happy to do with other troubling phenomena more widely accepted by the scientific community of his time. Thus, when Darwin repeatedly insists that pangenesis is the only hypothesis he knows that can explain the phenomena of generation and heredity, we should take him at his word and conclude that he failed to conceive of even the possibility of any common-cause alternative to pangenesis in the first place.

4 Galton and common-cause inheritance

By this point it will surely seem to some readers that I have already spilled an undue amount of ink defending the rather modest historical thesis that Darwin never conceived of the possibility of a common-cause mechanism of hereditary resemblance, but even this unassuming claim must still face at least one daunting historiographical challenge: how are we to reconcile it with the fact that the earliest expressions of the theory of the continuity of the germ plasm reach back perhaps as far as Richard Owen's 1849 work on parthenogenesis and in any case certainly to Francis Galton's 1865 article 'Hereditary Talent and Character' in Macmillan's magazine? There is no doubt that Darwin read Galton's article, for he refers readers of *Variation* (e.g. the

[15] See also Olby ([1985], p. 58, original emphasis): 'as Cowan admits . . . there was little *hard* evidence at that time in support of the inheritance of acquired characters'

American edition of 1868, v. ii, p. 16) to this 'very able paper on hereditary talent'. And the feature of Galton's paper most noted by historians of science is the following startling suggestion:

> We shall therefore take an approximately correct view of the origin of our life, if we consider our own embryos to have sprung immediately from those embryos whence our parents were developed, and these from the embryos of *their* parents, and so on forever. We should in this way look on the nature of mankind, and perhaps on that of the whole animated creation, as one continuous system, ever pushing out new branches in all directions, that variously interlace, and that bud into separate lives at every point of interlacement. (Galton [1865], p. 322)

We should not, however, make the mistake of assuming simply because Darwin read Galton's 1865 paper that he either recognized or understood the idea of the continuity of the germ plasm proposed therein. The central aim of the 1865 article was not to propose a mechanism or theory of inheritance at all, but instead to establish the noninheritance of acquired mental abilities in human beings and (to borrow Ruth Schwartz Cowan's appealing term) the 'omnicompetence' of heredity in determining human mental and moral characteristics.[16] Perhaps unsurprisingly, then, the use Darwin makes of this paper is only to suggest that while some 'have doubted whether those complex mental attributes, on which genius and talent depend, are inherited... he who will read Mr. Galton's able paper on hereditary talent will have his doubts allayed' [1868], v. ii, p. 16; the second edition ([1905], (v. i, p. 538) mentions instead, in an otherwise identical passage, 'Mr. Galton's able work on "Hereditary Genius", a reference to Galton's 1869 book of that name). This does not yet, of course, provide any evidence that Darwin failed to understand Galton's idea of the continuity of the germ plasm, but it does show why Darwin's mention and apparently favorable opinion of the 1865 article need not be taken as evidence of having considered or understood the paper's brief, tangential suggestion of germ line continuity.

Furthermore, there is indeed telling evidence of Darwin's failure to comprehend Galton's proposal of the continuity of the germ plasm in their exchange of correspondence of 1875, preceding Galton's presentation of his paper 'A Theory of Heredity' to the Anthropological Institute. Hearing of Galton's interest in the matter and impending publication, Darwin wrote in early November of 1875 to warn him of Huxley's distrust of the views of Balbiani (all the correspondence in this exchange can be found in Volume II

[16] Galton seeks to discharge this task in a remarkably dogmatic way, offering little in the way of scientific argument or evidence and much in the way of generalities, assurances, and eugenic fantasies. Indeed, Cowan ([1985], pp. 65–6) describes the 1865 article as 'a failure as a scientific treatise' and 'an exercise in political rhetoric' in arguing that both Galton's interest in heredity and his commitments on contentious matters of fact were rooted in his eugenic ambitions.

of Pearson's *Life Letters and Labours of Francis Galton* [1924], pp. 181–9). Galton's appreciative reply sought to summarize the contents of 'A Theory of Heredity', including his view that

> we must not look upon those germs that achieve development as the main sources of fertility; on the contrary, considering the far greater number of germs in the latent state, the influence of the former, i.e. of the personal structure, is relatively insignificant. Nay further, it is comparatively sterile, as the germ once fairly developed is passive; while that which remains latent continues to multiply. ([1924], p. 182)

By elaborating this view, Galton claims to account 'both for the fact, and for the great rarity and slowness of the inheritance of acquired modifications' ([1924], p. 182). He then suggests that the appropriate analogy for the relationship between parent and child is not that of parent country to colonists, but of the representative government of the parent nation to that of the colonists, under the supposition that a small proportion of the colonists are nominated to its government by the government of the parent country. With this, Galton says, he has 'so far as the limits of a letter admit, made a clean breast of my audacity in theoretically differing from Pangenesis', a difference he summarizes with the following two propositions:

> 1. In supposing the sexual elements to be of as early an origin as any part of the body (it was the emphatic declarations of Balbiani on this point that chiefly attracted my interest) and that they are not formed by aggregation of germs, floating loose and freely circulating in the system, and
> 2. In supposing the personal structure to be of very secondary importance in Heredity, being, as I take it, a *sample* of that which is of primary importance, but not the thing itself. ([1924], p. 183, original emphasis)

Although Darwin was 'delighted that you stick up for germs', he seems to have been unable to follow Galton's summary, saying only that he 'can hardly form any opinion until I read your paper *in extenso*' (and drawing Galton's attention to Brown-Séquard's latest experimental results supporting the inheritance of acquired characters and to 'the many cases of parthenogenesis'). He reports that he is 'very glad indeed of your work, though I cannot yet follow all your reasoning' (Darwin to Galton, Nov. 4, 1875; in [1924], p. 183). Galton responded to this invitation by sending Darwin one of the proofs of 'A Theory of Heredity' with the 'hope it will make my meaning more clear'. There again Galton had proposed the continuity of the germ plasm: he defined an organism's 'stirp' as 'the sum total of the germs, gemmules, or whatever they may be called, which are to be found, according to every theory of organic units, in the newly fertilized ovum—that is in the early pre-embryonic stage—from which time it receives nothing further from its parents, not even from its mother, than mere nutriment' ([1924], p. 185) and he argued that 'The stirp of the child may be considered to have descended directly from a part of the stirps of each of its parents, but then the personal structure of the child is no more than an imperfect representation of his own stirp, and the personal structure of each of the parents is no more than an imperfect representation of each of their own stirps.' ([1924], p. 186).

Darwin found the paper itself no easier to grasp and no less puzzling than Galton's summary had been. He writes,

> I have read your essay with much curiosity and interest, but you probably have no idea how excessively difficult it is to understand. I cannot fully grasp, only here and there conjecture, what are the points on which we differ—I daresay this is chiefly due to muddle-headiness[17] on my part, but I do not think wholly so. Your many terms, not defined 'developed germs'—'fertile' and 'sterile' germs (the word 'germ' itself from association misleading to me), 'stirp,'—'sept,' 'residue' etc. etc., quite confounded me... Unless you can make several parts clearer, I believe (though I hope I am altogether wrong) that very few will endeavor or succeed in fathoming your meaning. ([1924], p. 187)

What followed this letter of Nov. 7 was an exchange in which Darwin tried to explain the sources of his confusion and skepticism while Galton sought unsuccessfully to make his position clear to Darwin (see Cowan [1985], pp. 117–8). It appears from the letters that part of the dispute was mediated by George Howard Darwin, traveling between London and Down House representing the views of each correspondent to the other in person (see Darwin's letter of Dec. 18 and Cowan [1985], p. 118). At no point in this exchange did Darwin show any evidence of having resolved his initial perplexity or of understanding the idea of the continuity of the germ plasm that Galton sought to propose, and although he appreciated the gracious spirit in which Galton had received his earlier accusations of obscurity, he nonetheless persisted in finding his cousin's account of heredity opaque:

> I have this minute finished your article in Fraser[18] and I do not think I have read anything more curious in my life... I should be glad to be convinced that the obscurity was *all* in my head, but I cannot think so, for a clear-headed (clearer than I am) member of my family[19] read the article and was as much puzzled as I was. To this minute I cannot define what are 'developed,' 'sterile' and 'fertile' germs. You are a real Christian if you do not hate me for ever and ever.' (Darwin to Galton, Nov. 10, 1875; in [1924], pp. 188–9)

[17] ([1903], v. i, p. 360) has 'muddy-headedness.'
[18] *Fraser's Magazine*, in which Galton had published articles concerning heredity in 1873 and 1875.
[19] Alison Pearn of the Darwin Correspondence Project at Cambridge has suggested to me that this 'clear-headed' member of Darwin's family was probably his daughter Henrietta, to whom he often showed materials he wished to discuss.

Notice that in both this and Darwin's earlier letter to Galton, the specific terms Darwin singles out as central to his confusion are the ones at the heart of the common-cause character of the stirp theory itself: 'fertile' and 'sterile' germs, 'stirp' and 'residue'. Thus it does not seem plausible to suggest that in fact Darwin grasped Galton's fundamental idea of a common-cause account of inheritance and that it was instead some other aspect of the stirp theory he found so perplexing.

Of course, the central issue before us is not whether Darwin would have accepted Galton's proposed continuity of the germ plasm had he understood it—he almost certainly would not have, in part because he was increasingly convinced of the widespread existence and importance of the inheritance of acquired characters, which a continuous germ-line would have reduced to a special case or anomaly (see above). Furthermore, Darwin was looking for a theory of inheritance that would permit natural selection to function as the engine of evolution, and he took this to require allowing an important role for the inheritance of acquired characters (though see note 13 above). The point is instead that Darwin shows no evidence of having considered and rejected the idea that similarities between ancestors and offspring might be results of a common-cause rather than links in a causal chain, and instead gives every indication of being unable even to understand this line of thought when it was presented to him directly by Galton. The most natural conclusion to draw from the historical evidence is that Darwin simply failed to conceive of or consider the entire *class* of theoretical alternatives to pangenesis picked out by this idea, notwithstanding the fact that it offered equally compelling explanations for what he regarded as the central phenomena of inheritance and generation.[20]

Of course, the class of common-cause accounts of inheritance was not the *only* set of serious alternatives that escaped Darwin's notice, and the broader point here is not Darwin's failure to consider this specific set of hypotheses but rather his failure or inability to exhaust the space of serious alternative possibilities *generally*. Still, the importance and centrality of this particular set

[20] Note that while the class of common-cause alternatives neglected by Darwin certainly includes some members (like Mendelian or contemporary genetics) with particulate (in the sense of non-blending) heredity, we should not make the mistake of trying to support the problem of unconceived alternatives by appealing to the widespread presumption that a particulate conception of heredity was somehow the natural complement to Darwin's selectionist conception of evolution or the missing piece of a seamless puzzle and suggesting that Darwin would surely have embraced particulate heredity as the bride of natural selection if only he had thought of it. As Bowler argues convincingly ([1989], pp. 61–3), this suggestion depends upon a misreading of Darwin's response to Fleeming Jenkin's famous argument that blending inheritance makes evolution impossible (because characteristics that arose and were favored by selection would be swamped by blending in subsequent matings) and a misunderstanding of Darwin's commitment to both the gradual character of the process of evolution and the continuous (rather than saltational) character of the traits on which selection acted. For an extremely useful detailed discussion, see also Gayon ([1998], Ch. 3).

of possibilities both to one of Darwin's own contemporaries (Galton) and to immediately subsequent theorizing about inheritance and generation make it impossible to argue that it wasn't really a serious competitor even by the standards of his own day.

5 Conclusion

It is somewhat ironic (though not at all uncharacteristic) that Darwin adopted such an apologetic and self-deprecating stance about his inability to understand Galton's account, for Darwin was anything but alone among mid-19th century theorists in failing to grasp the fundamental structure of inheritance that Galton sought to propose. After all, the doctrine of the continuity of the germ plasm is most famously associated not with Galton but with August Weismann: although Weismann would later acknowledge that Galton had recognized the possibility of the continuity of the germ plasm, he was surely right to suggest that this idea had enjoyed virtually no attention and was of little significance for the scientific community at the time (Robinson [1979], p. 30). The proposal of germ-line continuity and the correlative idea that phenotypic continuities between ancestors and offspring might be the results of a common-cause rather than links in a causal chain was simply not a feature of the scientific landscape prior to Weismann's publication of it in 1883.

This fact helps to undermine what might otherwise seem a plausible response to the use I have made of this episode to try to support the general significance of the problem of unconceived alternatives. We might imagine an opponent pointing out that the real issue is whether *scientific communities* rather than individual scientists are good at exhausting the space of well-confirmed possibilities before proceeding to eliminative or abductive conclusions, and suggesting that this case simply shows that the broader scientific community of mid-19th century generation theorists (including Galton) was able to do this when Darwin alone could not. It is quite right to emphasize that any consequences for scientific realism here depend on the range of alternative possibilities that communities rather than individuals are able to effectively consider. But not only was recognition of the possibility of a common-cause account of inheritance not widespread among the members of any scientific community to which Darwin and Galton belonged, this theoretical possibility does not even seem to have been considered or recognized anywhere outside of Galton's own writings. Thus, Galton's proposal of a common-cause mechanism for inheritance is valuable to us largely because of how clearly Darwin's reaction to it reveals his failure to even comprehend this possibility, and not because it reveals anything about the ideas being seriously considered among mid-19th century theorists of generation and inheritance.

Moreover, it would be a profound mistake to suggest that together Darwin and Galton managed to conceive of the full range of *even just those common-cause* accounts of inheritance and generation that were both well-confirmed by the available evidence and sufficiently scientifically serious as to be ultimately accepted by later scientific communities. It is true that Darwin failed to conceive of the entire class of common-cause theories of generation or inheritance and was therefore unable to even understand the particular representative member of this class that Galton put forward. But as I document in detail elsewhere (Stanford [2006], Ch. 4), Galton's case for the stirp theory reveals that even as he managed to recognize one member of this general class of alternative possibilities, he failed in turn to conceive of many *further* members of *this very class* that were themselves both well-confirmed by the evidence available to him and sufficiently scientifically serious as to be ultimately accepted by later scientific communities.

Thus, I think we must ultimately recognize this case as providing impressive support for the importance of a quite general challenge to scientific realism that rests neither on the speculative possibility that there are scientifically serious empirical equivalents to any and all theories, nor on the simple fact that past successful theories have turned out to be false. For decades Darwin applied a first-rate mind to the search for some convincing explanation of the hereditary phenomena of interest to him, but he failed to conceive of even the broad possibility that similarities between parents and offspring were the products of a common-cause rather than links in a causal chain. And if I am right to suggest that the historical record has the general character suggested by this single example, we would indeed do well to worry about what well-confirmed and scientifically serious alternative theoretical possibilities remain unconceived by scientists of the present day.

Despite the reasons I offered at the outset of our inquiry to think that any evidence of the problem of unconceived alternatives we found in this case might be particularly telling, it should be clear that a single example can do no more than illustrate the character of the problem and make its general significance seem plausible. But if we do find that the historical record is characterized more generally by the pattern evidenced in this single detailed example, this will indeed call into serious question the sort of eliminative or abductive support we are typically in a position to offer for even the best of the fundamental theoretical accounts we have of otherwise inaccessible domains of nature. As we noted earlier, eliminative or abductive inferences are capable of reaching true conclusions only when the truth is among the possible alternatives under consideration or the candidate explanations for a set of phenomena with which they begin. Thus, if the historical record of scientific inquiry itself reveals that scientists and scientific communities routinely fail to conceive of the sorts of well-confirmed alternative theories that are sufficiently scientifically serious as to be embraced by later scientific communities, then we cannot responsibly infer that the best or only explanation we ourselves can offer of the phenomena in some otherwise inaccessible domain of nature is even likely to represent the truth of the matter. Although eliminative and abductive inferences might still have much to recommend them as important tools for inquiry even in the course of our fundamental theorizing about otherwise inaccessible domains of nature, we will have discovered that this specific epistemic context is one in which we cannot justifiably regard the products of such eliminative or abductive inferences as even probably or approximately true.

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Department of Logic and Philosophy of Science
University of California
Irvine, 5100 Social Science Plaza
Irvine, CA 92697-5100
USA
stanford@uci.edu

References

Bowler, P. J. [1989]: *The Mendelian Revolution: The Emergence of Hereditarian Concepts in Science and Society*, Baltimore: Johns Hopkins University Press.

Churchill, F. B. [1987]: 'From Heredity Theory to *Vererbung*: The Transmission Problem, 1850–1915,' *Isis*, **78**, pp. 337–64.

Cowan, R. S. [1985]: *Sir Francis Galton and the Study of Heredity in the 19th Century*, New York: Garland Publishing.

Darwin, C. [1868]: *The Variation of Animals and Plants Under Domestication*, 1st American edition, 2 volumes, New York: Orange Judd and Co.

Darwin, C. [1903]: *More Letters of Charles Darwin*, 2 volumes, in F. Darwin and A. C. Seward (*eds*), London: John Murray.

Darwin, C. [1905]: *The Variation of Animals and Plants Under Domestication*, 2nd edition, 2 volumes, London: John Murray. Originally published in 1874. The first edition of this work was published in 1868.

Darwin, C. [1959]: *The Life and Letters of Charles Darwin*, 2 vols., in F. Darwin (*ed.*), New York: Basic Books. Originally published in 1887.

Darwin, C. [2002]: *The Correspondence of Charles Darwin. Volume 13*, in F. Burkhardt, M. Porter, S. A. Dean, S. Evans, S. Innes, and A. M. Pearn (*eds.*), Cambridge: Cambridge University Press.

Dunn, L. C. [1965]: *A Short History of Genetics*, New York: McGraw-Hill Book Company.

Duhem, P. [1954]: *The Aim and Structure of Physical Theory*, translated from the second edition by Philip P. Wiener, Princeton: Princeton University Press. Originally published in 1914 as *La Théorie Physique: Son Objet, et sa Structure*, Paris: Marcel Rivièra & Cie.

Endersby, J. [2003]: 'Darwin on Generation, Pangenesis, and Sexual Selection,' in J. Hodge and G. Radick (*eds.*), *The Cambridge Companion to Darwin*. Cambridge: Cambridge University Press, pp. 69–91.

Galton, F. [1865]: 'Hereditary Talent and Character,' *McMillan's Magazine*, **12**, pp. 157–66, 318–27.

Gayon, J. [1998]: *Darwinism's Struggle for Survival: Heredity and the Hypothesis of Natural Selection*, Cambridge: Cambridge University Press.

Gasking, E. B. [1967]: *Investigations Into Generation: 1651–1828*, Baltimore: Johns Hopkins University Press.

Geison, G. [1969]: 'Darwin and Heredity: The Evolution of His Hypothesis of Pangenesis,' *Journal of the History of Medicine*, **24**, pp. 375–411.

Hodge, M. J. S. [1985]: 'Darwin as a Lifelong Generation Theorist,' in D. Kohn (*ed.*), *The Darwinian Heritage*, Princeton: Princeton University Press, pp. 207–43.

Hodge, M. J. S. [1989]: 'Generation and the Origin of Species [1837–1937]: A Historiographical Suggestion,' *British Journal for the History of Science*, **22**, pp. 267–81.

Olby, R. C. [1963]: 'Charles Darwin's Manuscript of Pangenesis,' *British Journal for the History of Science*, **8**, pp. 85–93.

Olby, R. C. [1985]: *Origins of Mendelism*, 2nd edition, Chicago: University of Chicago Press. The first edition was published in 1966.

Pearson, K. [1924]: *The Life, Letters and Labours of Francis Galton, Volume Two: Researches of Middle Life*, Cambridge: Cambridge University Press.

Robinson, G. [1979]: *A Prelude to Genetics: Theories of a Material Substance of Heredity, Darwin to Weismann*, Lawrence, KS: Coronado Press.

Spencer, H. [1864]: *Principles of Biology*, 2 volumes, London: Williams and Norgate.

Stanford, P. K. [2001]: 'Refusing the Devil's Bargain: What Kind of Underdetermination Should We Take Seriously?' *Philosophy of Science*, **68**, pp. S1–S12.

Stanford, P. K. [2006]: *Exceeding Our Grasp: Science, History, and the Problem of Unconceived Alternatives*, New York: Oxford University Press.

Winther, R. G. [2000]: 'Darwin on Variation and Heredity,' *Journal of the History of Biology*, **33**, pp. 425–55.