

## **Darwin's Pangenesis and the Problem of Unconceived Alternatives**

### **Abstract**

P. Kyle Stanford has 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 Stanford's challenge.

### Introduction

P. Kyle Stanford (2001; forthcoming) has argued that the most significant threat to scientific realism derives neither from traditional underdetermination arguments nor from the traditional pessimistic induction, but from a quite different sort of historical pattern. What should actually give realists pause, he suggests, 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 (as opposed to, say, Cartesian fantasies). Of course, a 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. But if the historical evidence confirms that past practitioners have routinely failed to conceive of (and therefore failed to consider) such alternatives when they existed, we have every reason to believe that there are similarly serious and well-confirmed unconceived alternatives to contemporary scientific theories, even if we cannot specify or describe them further. Of several advantages over the pessimistic induction, perhaps the most important is that this problem of unconceived alternatives concerns the theorists rather than the theories of past science: even if contemporary scientific theories sometimes enjoy confirming 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.

Although Stanford offers a long list (2001 S9) of examples of historical progressions of theories that he suggests exemplify this problem of unconceived alternatives, he acknowledges that his case must 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 evaluating the significance of Stanford's challenge by examining just one of his examples in this 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 Stanford's contention that the problem of unconceived alternatives poses a clear and present danger to scientific realism.

I choose this example not only because it is one that Stanford mentions explicitly in connection with his claim, but also 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 importantly 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.

#### Darwin and Pangenesis: The Search for the Material Basis of Generation and Heredity

From the middle to the end of the 19<sup>th</sup> 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 34; Olby 1966 55; Robinson 1979 xiii, 3; Cowan 1985 Ch. 5; Bowler 1989 46; Gasking 1967 161; Geison 1969 375, 385-6).<sup>1</sup> Though various kinds of hereditary particles had been proposed by Buffon,

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<sup>1</sup> 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

Diderot, Maupertuis and others in the period before Darwin, the idea of living or material units or particles<sup>2</sup> 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 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 or VAP).<sup>3</sup> Although Spencer’s version of this general idea was published four years earlier, Darwin’s account seems not to have been based on it in any way,<sup>4</sup> having been by that time under construction for some twenty-odd years.<sup>5</sup> In any

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.

<sup>2</sup> 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). ~~Thus, while views like Darwin’s and Spencer’s certainly involved the postulation of material particles inherited by offspring from parents, they were not~~ we will see that these were not particulate views of heredity in this important sense.

<sup>3</sup> 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

<sup>4</sup> See Darwin to Hooker, February 23 [1868] in Life and Letters of Charles Darwin (1959 [1887]; hereafter LLD) ii 259-61; and Darwin to Wallace, February 27 [1868] in LLD ii 262). As a general matter ~~Indeed~~, the similarities between Darwin’s account and any number of earlier ~~particulate~~ 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 LLD ii 228, Darwin to Huxley, [1865?] in LLD ii 228-9, and Darwin to Ogle, March 6 [1868] in LLD ii 265): the pangenesis manuscript of 1865 contained no mention of related earlier theories, the first edition of VAP discussed those of Buffon, Bonnet, Spencer, and Owen, and the second addition added mention of more views “nearly similar” to pangenesis by Hippocrates, Ray, and a Prof. Mantegazza (VAP ii 457n; see Geison 1969 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-19<sup>th</sup> Century: as Geison notes, “Darwin could probably have demonstrated... fundamental differences between his ideas and those of any of the pre-nineteenth century pangenetic theorists” (1969 395).

<sup>5</sup> In August of 1867 Darwin wrote to Charles Lyell “I do not know whether you have ever

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 343).

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 343-5; Bowler 1989 25, 68; for an especially clear expression from Darwin himself, see VAP ii 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 that "we may on the whole conclude that inheritance is the rule, and non-inheritance the anomaly" (VAP ii 454) and that the "proper function" of reproductive systems is "transmitting truly the characters of the parents to the offspring" (VAP ii 453). Against this theoretical background, here is Darwin's own description of pangenesis as it appeared in the second (1874) edition of the Variation:

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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 LLD ii 255). Further [compelling evidence](#) that Darwin was a "lifelong generation theorist" [is provided by Hodge \(1985; discussed in Bowler \(1989 58\); 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 1966 118).

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. (VAP ii 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 (VAP ii 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. (VAP ii 432-433).

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” (VAP ii 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” (VAP ii 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” (VAP ii 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 a 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” (VAP ii 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

pangeneses 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 LLD ii 264).

Besides illustrating his reasons for thinking that vitalistic appeals offered at best an intolerably vague description of the sort of mechanism posited by pangeneses 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 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 LLD ii 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 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 [VAP] 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 LLD ii 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 LLD ii 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 LLD ii 262 and in More Letters of Charles Darwin (hereafter MLD) i 301). To Hooker he quotes Wallace<sup>6</sup> 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,

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<sup>6</sup> From a letter written to Darwin himself; February 1868 in MLD i 300.

February 28 [1868] in LLD ii 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 MLD ii 371). And he writes to Fritz Müller that “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 MLD ii 82).<sup>7</sup> 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 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.<sup>8</sup>

Given Darwin’s apparent inability to conceive of any alternative to pangenesis’ basic 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

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<sup>7</sup> As late as 1873 Darwin confessed to A. 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 MLD i 348).

<sup>8</sup> 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.

Hooker, February 3 [1868] in LLD ii 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 LLD ii 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 LLD ii 256), to F. Hildebrand that he believes it “will ultimately be accepted” (Darwin to Hildebrand, January 5 [1868] in MLD i 285) and to Müller that “Pangeneses will turn out true someday!” (Darwin to Müller, May 12 [1870] in MLD ii 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 LLD ii 265) and to J. J. Weir that “I fully believe pangeneses will have its successful day” (Darwin to Weir, March 17 [1870] in MLD i 320). The Calendar of Darwin’s correspondence (Burkhardt, et al, 1994) also describes letters (not included among those published to date) expressing his sentiments to J. V. Carus that he “believes physiologists will some day be compelled to admit some such doctrine” (October 19 [1867]), and to Hooker that he is “still convinced it will be hereafter looked on as ‘best hypothesis of generation inheritance & development’” (July 14 1868).<sup>9</sup> It seems hard to explain this assurance that pangeneses would ultimately triumph without assuming that its source lies in what he elsewhere frankly admits: that he can think of no other mechanistic hypothesis that can account for the phenomena.

Moreover, Darwin explicitly links his confidence that pangeneses will triumph or reappear with his inability to identify any alternative explanation for what he considered

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<sup>9</sup> Quotations in this sentence are from the descriptions of the contents of the letters found in the Calendar, not from Darwin himself.

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 LLD ii 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 truly or falsely is another question,<sup>10</sup> by Pangenesis. (Darwin to Hooker, February 23 [1868] in LLD ii 261, original emphasis).

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

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<sup>10</sup> This reservation is somewhat surprising, for in another letter to Hooker just five 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 LLD ii 264; see above).

mechanical explanation of the phenomena of generation and 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 MLD ii 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 (VAP ii 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)<sup>11</sup>), 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

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<sup>11</sup> Such ~~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 VAP ii 446, MLD ii 359), folk wisdom, the stories of animal breeders, and the like (see Olby 58-9 and 94, 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.

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,<sup>12</sup> 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” (VAP ii 70-71) 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’

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<sup>12</sup> A note of caution is in order here, however. As Winther documents (2000 436-9), Darwin felt was increasingly forced to make room in his theory for a source of systematic, directed, nonrandom, 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) 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 439). Thus, while Darwin was certainly convinced (along with many other naturalists of the 19<sup>th</sup> 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.

alternative to pangenesis), a separate, gemmule-mediated 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"; VAP ii 455, 486), but he has very little in the way of a substantive account to offer (see VAP ii 357) of why or the mechanism whereby they do so.<sup>13</sup> 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 388-91, 410), 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

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<sup>13</sup> Darwin seems to recognize this, concluding merely that we have gained "some insight" (VAP ii 488) into distant reversion and ultimately that "[r]everision depends on the transmission from the forefather to his descendants of dormant gemmules, which occasionally become developed under certain known or unknown conditions" (VAP ii 491). In the pangenesis manuscript of 1865 he simply attributes distant reversion to "unknown causes" (Olby 1963 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 MLD ii 339-340). 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 1966 66) 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 MLD ii 339-340). Nonetheless, Darwin does explicitly follow Naudin's account of reversion in the offspring of ordinary hybrids in VAP ii 486-7.

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” (VAP ii 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 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 (ii 462) and that it has no explanation for a number of differences in tendencies to reversion between plants propagated from buds rather than seeds (ii 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 MLD i 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” (MLD i 302).

Finally, unlike the evidence for most or perhaps all of the other phenomena for which Darwin introduced pangenesis as an explanation, the very existence of the inheritance of acquired characteristics was a controversial empirical matter even at the time Darwin wrote. Perhaps the most influential support for the phenomenon came from famous experiments on guinea-pigs by the physiologist Brown-Séquard (see VAP ii 483; Robinson 1979 22; Cowan 1985 63-4). But Geison points out that “opinion was divided among influential 19<sup>th</sup> Century authors,” noting that James Cowles Pritchard, William Lawrence, and Joseph Hooker, for example, seem to have denied that the phenomenon occurred (1969 379n). Olby goes much further, claiming that it was “widely held” at the

time that acquired characters are not inherited (1966 61).<sup>14</sup> Not only did Darwin know 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]henver 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 MLD i 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 explanation 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

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<sup>14</sup> Note, however, Cowan’s competing claim that “almost all reputable biologists...were prone to accept” the inheritance of acquired characteristics (1985 62-3).

first place.

### 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 (see Thompson 1888-9, cited in Robinson 1979 30n) 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 VAP (e.g. the American edition of 1868) to this "very able paper on hereditary talent" (ii 16). 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 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.<sup>15</sup> 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" (VAP (first American edition, 1868) ii 16; the second edition of VAP (i 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

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<sup>15</sup> 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 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.

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 Pearson’s Life Letters and Labours of Francis Galton (hereafter LLL) 1914-1930 ii 181-189). 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. (LLL ii 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” (LLL ii 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. (LLL ii 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-Séguard’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 LLL ii 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” (LLL ii 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.” (LLL ii 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-headedness<sup>16</sup> 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. (LLL ii 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 117-118). It appears from the letters that part of the dispute was mediated by George Howard Darwin, traveling between London and Down representing the views of each correspondent to the other in person (see Darwin's letter of Dec. 18 and Cowan 1985 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:

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<sup>16</sup> MLD i 360 has “muddy-headedness.”

I have this minute finished your article in Fraser<sup>17</sup> 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 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 LLL ii 188-9)

The irony in this situation, of course, is that Darwin was anything but alone 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 acknowledged 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 30). The doctrine of the continuity of the germ plasm 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.

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

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<sup>17</sup> Fraser’s Magazine, in which Galton had published articles concerning heredity in 1873 and 1875.

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 12 above).<sup>18</sup>

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 indeed shows no evidence of even having been able to understand this line of thought when it was presented to him directly by Galton. Instead 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.<sup>19</sup>

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<sup>18</sup> 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 61-63), 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.

<sup>19</sup> 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 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 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 by

### Conclusion

I suggested above some reasons to suspect that finding evidence of the problem of unconceived alternatives in this case might constitute a reason to think the problem itself to be of quite general significance. But whether or not that claim is established I think we must regard this case as providing substantial support for Stanford's challenge: 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 Stanford is right to suggest that the historical record has the general character suggested by this single detailed example, then he is also right to suggest that the central challenge to scientific realism really is that posed by the possibility of equally well-confirmed and scientifically serious alternatives to our own theories which nonetheless remain unconceived by scientists of the present day.

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the standards of the time.

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