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## The Darwin of pangenesis

*Le Darwin de la pangénèse*

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## ABSTRACT

The Darwin of pangenesis is very much another Darwin. Pangenesis is Darwin's comprehensive theory of generation, his theory about all sexual and asexual modes of reproduction and growth. He never explicitly integrated pangenesis with his theory of natural selection. He first formulated pangenesis in the 1840s and integrated it with the physiology, including the cytology, of that era. It was, therefore, not consistent with the newer cytology of the 1860s when he published it in 1868. By reflecting on the role of pangenesis in Darwin's life and work, we can learn to take a wider view of his most general theorising about animal and plant life.

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## R É S U M É

Le Darwin de la pangénèse est véritablement un autre Darwin. La pangénèse est sa théorie globale de la génération, sa théorie de l'ensemble des modes de reproduction sexués et asexués, et de la croissance. Il ne l'a jamais explicitement articulée avec sa théorie de la sélection naturelle. Il la formula d'abord dans les années 1840, et l'a articulée avec la physiologie et la cytologie de cette époque. La pangénèse n'était donc pas en phase avec la nouvelle cytologie des années 1860 lorsqu'il en publia l'exposé en 1868. En examinant le rôle de la pangénèse dans la vie et l'œuvre de Darwin, nous pouvons accéder à une vision plus large de ses théorisations les plus générales de la vie animale et végétale.

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## 1. The Darwin of pangenesis is alien, other, not one of us

There is the Darwin of *On the Origin of Species* (1859). That book presents, throughout, a single but not simple theory of species origins: common descent by means of natural selection – branching natural selection for short. The Darwin of the *Origin* is the Darwin of natural selection. The other Darwins are the Darwin of sexual selection, for example, or of earthworms or coral reefs and so on. One of these other Darwins is the Darwin of pangenesis. This was Darwin's theory of generation, where generation includes every instance of living matter – plant or animal – making

more of itself: in sexual reproduction, in asexual budding, or in healing wounds or in ordinary growth. Natural selection and pangenesis were Darwin's only two completely general theories comprehending all animals and plants; and they were general biological theories, for neither is a theory about the physics or about the chemistry of life. The analysis given in the present paper seeks to elucidate two apparently contradictory themes about the Darwin of pangenesis: the central place of generation theory for Darwin's entire life as a scientist, and, yet too, the lack of any integration of pangenesis and natural selection. The analysis is presented as an interpretative historical essay rather than as a scientific paper, so the references are confined to a bibliographical note at the end.

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Pangeneses was first published in 1868 in the final chapter of Darwin's two volume treatise on *The Variation of Animals and Plants Under Domestication*; and it was republished, with no significant changes, in 1875 in the second edition of that treatise. Pangeneses is usually introduced, as it is by Darwin himself, by giving its summary account of sexual reproduction in higher animals. Such an account says that every part of the body of each parent, male or female, produces tiny, invisible buds or gemmules. These gemmules are then transported to the sexual organs, the gonads. At fertilisation, two lots of these gemmules come together to form a fertile ovum from which the offspring grows and develops.

There is nothing misleading in introducing pangeneses in this summary way, and the introduction has two virtues. First, the rationale for the name pangeneses is easily grasped, because this introduction makes explicit the claim that the offspring is a product of the whole of a parent organism. Second, the contrast with what has been taught to students throughout the twentieth century and on into the twenty-first is plain to see. For those students have been taught that the offspring is not derived from the whole bodies of its parents, but only from reproductive cells in a cell lineage going back to the fertilised egg cell that each parent was once. For Darwin, an offspring resembles a parent in every part because it is produced from buds from every part. For those students, this resemblance is explained quite otherwise: the resemblance is due to the offspring's development being influenced by the same cause that influenced the parent's development, namely the materials in the fertilised egg cell from which the parent grew. For those materials are also in the egg cell from which the offspring grew.

So the Darwin of pangeneses is another Darwin in this sense too. His views are totally alien to what has been taught to students for over a century now: totally alien to the orthodox cellular biology, the standard cytology, for sexual reproduction in higher animals. The Darwin of pangeneses is not one of us, he is another.

This sense of the otherness of the theory of pangeneses is enhanced even more if we look in summary not at what it says about sexual reproduction in higher animals or asexual reproduction in lower plants, but about all kinds of reproduction, about all generation. To engage with these most general theses is entirely apt, because, as Darwin himself emphasises repeatedly, the principal aim of the theory was to propose just such general, unifying theses about all generation.

In all generation, Darwin holds, the observable powers are the same and so, too, the unobservable matter. There is no exclusive association of maturation, fertilisation and impressionability with sexual rather than asexual modes of reproduction. For, aphid parthenogenesis shows us an unfertilised ovum producing a maturing offspring with no prior interaction with a male element. Again, graft hybrids and the effects of pollen on non-germinal tissue in a female plant both show impressionability – the ability to impress and to be impressed by variant characters – without observable fertilisation and maturation; while sporting and reversion in asexual plant buds show variation without observable fertilisation or maturation. All the

tiny, unobservable gemmules of pangeneses, in every mode of generation, are then credited by Darwin with all the powers required to explain the full extent of these observable powers. All living matter reproduces by producing microbuds, microgemmae, gemmules which are all capable of unobservable micromaturations, microfertilisations and so microimpressionabilities. In this way, pangeneses proposes a thesis of the unity in the material and the powers of all generations.

## 2. Pangeneses is not integrated by Darwin with natural selection

So, pangeneses is a unifying theory of generation. But is it a unifying theory in a broader way? Does Darwin integrate pangeneses with natural selection in a grand unification? No: very strikingly, he does not. Although common descent is discussed briefly in the pangeneses chapter, natural selection is not mentioned. Moreover, even in preparing the sixth edition of *Origin*, which appeared in 1872, four years after the first edition of *Variation*, he included no mention of pangeneses. Strikingly, in no known writing by Darwin, published or unpublished, is there any explicit integration of these two theories. The Darwin of pangeneses is indeed another Darwin, a Darwin other than the Darwin of the *Origin*, of natural selection.

But surely it was the same person, the same Charles Darwin, who formulated these two theories? And surely the theories themselves are manifestly connected; for natural selection is a theory about the selective fate of hereditary variations, while pangeneses is a theory, inter alia, about the generative production of that hereditary variation. Must not Darwin's historians assume that despite Darwin's reluctance to integrate them, the two theories were unified in his thinking if not in his writing? Must there not have been a unity in Darwin's thought, although not in his discursive expositions of that thought?

As so often in Darwin's case, the answers to these questions are complicated, and depend very much on which Darwin we are talking about: the composer of the public, published books of the 1850s, 60s and 70s, or the earlier author of the private, notebooks of the 1830s and 40s. However, before we engage those issues about Darwin himself, it is worth considering what expectations about unifications we may have concerning the sciences of life at this period.

Consider, first, not Darwin's intellectual biography but the much larger topic of the sciences of life in the nineteenth century. It is a familiar observation that the several announcements around 1800 of a new single science of life ("*biologie*," for example, as announced by Lamarck), were not followed in the rest of that century by any coordinated, consensual development of a single unified science of life. Indeed, at the close of the century, the American cytologist, Edmund B. Wilson, insisted that in biological theory, there was an obvious and fundamental division. Look, he urged, at the two most recent general biological theories to be established in that century: the theory of evolution and the theory of cells. Each, he says, has emerged from quite separate scientific endeavours and each addresses quite distinct domains. Evolution, as a

theory, is about the coming and going of species over vast spans of time and space; it is a theory arising from researches on voyages and in museums, researches in natural history.

By contrast, cytological theory – the theory of growth and development by cell divisions and differentiations – is not about species but about individuals, in health and disease, as studied in laboratories, in experiments and with microscopes, often in medical institutions, and so it is a theory that has arisen within physiology rather than natural history. The unification of evolutionary and cytological science requires, therefore, Wilson insists, active construction, for it is not secured merely by juxtaposing these two achievements; and he identifies August Weismann's theory of germ plasm continuity as offering the most promising bridge between them.

Even this brief sketch of Wilson's discussion of the actual disunity and potential unification of the nineteenth-century life sciences can prompt reflections on the intellectual-biographical challenge represented by the Darwin of pangenesis. A plausible scheme readily presents itself: there was a natural-historical Darwin, protégé of Henslow and Lyell, a theorist of the generation of species by means of branching natural selection, and author of the *Origin*. And there is a physiological Darwin, another Darwin, protégé at Edinburgh of Robert Grant, the Darwin who was the theorist of individual generations – and organ, tissue and cell generations – and author of the pangenesis chapter.

This scheme for the division of Darwin's theoretical labours is not unacceptably distorting. However, it does need qualifying with complicating modifications if it is not to mislead us. For, as so often in intellectual-biographical matters, issues of timing, sequence and succession have implications too consequential to be ignored. There is an asymmetry, an imbalance, a lack of equivalence between the *Origin* and the pangenesis chapter. No reader of the *Origin* thought that its author was out of date, out of touch, in any of those fields of inquiry – insect instinct studies, embryology, paleontology and the rest – that Darwin was drawing on and contributing to throughout the book. By contrast, it was manifest to physiologists reading the pangenesis chapter that Darwin was no master of their science's most comprehensive general theory: the theory of cells as it had been developing over the three decades since Schleiden's and Schwann's researches in the 1830s.

What those physiological readers could not know – but Darwin's historians can know today – is that the reason for this lack of cytological mastery in Darwin was simple enough. In the late 1830s and early 1840s, especially thanks to his reading in the English translation of Johannes Müller's treatise on human physiology, Darwin had been well versed in the cytology of that day. However, since then he had not kept up to date. Indeed, in 1865, when Darwin sent T.H. Huxley a draft of his pangenesis chapter, it seems that Huxley (who was knowledgeable about the newer, largely French and German, cytology), saw the need for Darwin to study recent authors such as Virchow and for Darwin to integrate pangenesis with their cell-theoretic doctrines. And Darwin, it seems, did then do that reading and did cite those doctrines in the published chapter.

However, these citations did not resolve the difficulty. Pangenesis had been formulated by Darwin in the early 1840s, in conformity with the cytology of that time, and he was not prepared to reconstruct it to conform it to the cytology of the 1860s. Unlike the old cytology of the 1830s, this new cytology of the 1860s required that new cells only arise from divisions of prior cells. Darwin's pangenesis has cells arising from subcellular gemmular material, a thesis acceptable perhaps to cytologists in the 1830s but not in the 1860s.

The conflicts of pangenesis with the newest cytology, especially concerning fertilisation, were even more obvious and extensive in 1875 when *Variation* appeared in its second edition. Many cytologists accepted now that each animal gamete is a single cell and that two fuse to form a fertilised ovum. Pangenesis has the fertilised ovum arising from the conjunction of two masses of subcellular gemmules.

We have here then further senses in which the Darwin of pangenesis is another Darwin. The *Origin* and natural selection are on one side, the natural history side, of a great divide in the sciences of life in the 1860s. Pangenesis is on the other side, the side of physiology. Moreover, the physiology of the 1860s is for Darwin not his own home; to some extent it is another country that he needs help communicating with through intermediaries such as Huxley. So, in the pangenesis chapter, we are reading a Darwin who has long given inquiries into generation a high priority and central place in his life a scientific theorist, and yet this is a Darwin who has parted company from those physiologists whose teachings constitute the authoritative consensus of this new age.

### 3. Integrations and disintegrations over the decades

Robert Grant gave Darwin, when a student at Edinburgh, his enduring concern with comparing and contrasting sexual and asexual modes of generation. Reading Charles Lyell's long and numerous chapters on species when on the *Beagle* voyage later gave Darwin his enduring concern with species, their births, lives and deaths over geological eons. These two concerns came together when, still voyaging, Darwin broke with Lyell about the causes of some species extinctions. Lyell ascribed all species extinctions to competitive upsets caused by slight changes in climate and other geographical circumstances. Darwin thought some extinctions were not due to such external circumstances, but to the ending of a limited species duration analogous to an individual's limited life duration. This conjecture led Darwin to suppose that sexual and asexual modes of generation were alike in transmitting a limited duration of life. In July 1837, now in London, Darwin's first extensive theorising about the formation of new, descendent species, from older ancestral species, was explicitly founded in a contrast between sexual and all other modes of generation. Only in sexual generations are there, he insisted, the maturations and fertilisations that make possible the cumulative, adaptive variations and divergences over successive generations which cause the reiterated species formations by which has grown the tree of life.

Over the following months, Darwin's species formation theorising is mingled constantly with his reflections on the peculiarities of sexual generation. The first sign that Darwin saw generation as a separable subject comes in early September 1838. He then adopts a new notebook practice. From now on, his notes on generation are not entered, along with reflections on other topics, in the main body of the *Notebook D* as they had been so far, but in pages at the end. It is not easy to discern any reason for this new practice. The best guess is suggested by the striking increase in the number and extent of his notes devoted to generation. It seems that the subject was concerning him in such an intense and extensive way at this time that he felt a need to give it its own space unmingled with his notes on other subjects. This guess is consistent with what is evident from those separate pages devoted to generation. For what those notes do is to carry on the quest for a fuller understanding of how sexual generation, through its distinctive fertilisations and maturations, enables the acquisition and transmission of adaptive variation. So the subject of generation at this time still has its central place in Darwin's theorising about species formations in the tree of life.

However, over the next three months, two developments do change relations between his thinking about generation and his thinking about the birth and death of species. The first development comes with Darwin's reading of Malthus on population. For reflecting on this reading leads Darwin right away to give up his generational theory of species deaths from the ending of limited species lifetimes. Darwin now reverts to Lyell's theory of species competitive defeats. The second development comes in November and December: the first elaboration of the theory of natural selection. This theory was understood from the start to be grounded in the analogy between man's and nature's selective breedings. It was in itself not a generational theory, rather, in its appeal to the struggle for existence arising from Malthusian population pressure, it is, like Lyell's theory of extinction – that Darwin had just returned to – a geographical and economy of nature theory, an ecological theory as we would say today.

These two developments did not give Darwin any reason for disconnecting his thinking about species births and deaths and individual generations, sexual and asexual. Indeed, he continues to inquire into generations of all kinds with the old aim of showing how sexual generation uniquely contributes to adaptive species formation and so to the generation of the tree of life. However, it was not long before this inquiry subverted itself. For, by 1841–2 it seems, Darwin had come to reject the whole notion that sexual reproduction was unique in the fertilisations and maturations that make it a necessary cause of all adaptive change in the long run of generations. As far as we can tell pangenesis was born, around 1841–2, from this rejection.

It seems that he first articulated the theory then with the same fundamental aim that he will have in 1868: to show that the observable powers of all generations are the same, and they are so because the unobservable material agencies and processes are too. Beyond this probable conjecture as to why and how Darwin arrived at pangenesis in the early 1840s, we can only proceed by

further, less probable, conjectures. One conjecture is that is among Darwin's most decisive reflections were those on graft hybrids. For, as he would emphasise later, graft hybrids appear to present clear cases of asexual organs and tissues interacting in quasi-fertilisational ways, by joining in impressing characters in producing a joint product. Another conjecture is a much more general. At the time, Darwin most probably first formulated pangenesis he would have seen himself as well up to date with physiological researches. By then, he had studied carefully the two volumes of the English translation of Müller's treatise on human physiology, and would have judged that this study had given him authoritative access to the state of physiology, especially in the leading nation, Germany, where Müller was the doyen of that science.

There is a complication, however. Darwin's attitude on subjects such as reproduction animals and plants was not entirely what these last remarks about his reading of Müller might suggest. Darwin did not think that the latest, authoritative writings made all older literature by lesser figures useless. For, he also seems at this time to have sought instruction and inspiration in rereading, for example, his grandfather's books; and it is likely that in arriving at pangenesis he drew on eighteenth-century as well as on more recent doctrines.

We have needed to resort to conjectures in reconstructing the origins of Darwin's theory of pangenesis and its initial motivating context in the early 1840s. But we are not guessing when we conclude that the theory as presented to the public in 1868 was still very much a child of that earlier time in Darwin's life and work. For there is every reason to believe that, once reached, then the leading theses constituting the theory were not revised significantly over the intervening decades.

This early origin for pangenesis explains why, when it was published, no prominent physiologist ever endorsed it as consistent with the best science of the day.

Even Hugo De Vries, who would never explicitly condemn it as totally erroneous, adopted only some of its essential proposals, while dropping others and constructing an alternative 'intracellular pangenesis' that was cytologically orthodox as Darwin's extracellular pangenesis was not. Pangenesis was therefore given a reception very unlike any other contribution to science that Darwin offered the world: it was often perceived not as too novel for comfort but as too archaic for assimilation to the best new science of the day. Here then is another sense in which the Darwin of pangenesis is another Darwin contrasting notably with the Darwin of the *Origin*.

#### 4. Conclusion

The Darwin of pangenesis is rewarding to study but for some reasons not others. Biologists in our time sometimes return to the nineteenth century for inspiration and instruction in putting right what they do not like about today's orthodoxies. A prominent case of such a quest is seen in the so-called 'evo-devo' literature: the writings of those current biologists who wish to integrate evolutionary and embryological concepts in a novel new synthesis, to achieve a synthesis such as was not, they complain,

achieved by the now-old ‘new evolutionary synthesis’ of the mid-twentieth. Could the Darwin of pangenesis contribute to this ‘evo-devo’ ambition? I do not think so. It is not merely that there is almost no comparative embryology in Darwin’s pangenetic theorising; there are those more fundamental difficulties raised by the lack of consilience with the orthodox cytology which even ‘evo-devo’ mavericks are not willing to jettison. So, as a resource for the scientists of today, pangenesis is unpromising. Quite generally, the Darwin of pangenesis fits uneasily in scientists’ history of science, much more comfortably in historians’ history of science. For historians, if not for scientists, it is indispensable to any quest for broader views and deeper insights concerning the full range of Darwin’s life and work, and their endless contextual complexities. In discussion, the divergences between historians’ history of science and scientists’ history of science can be negotiated, even perhaps reconciled, but never eliminated. Just why does Darwin’s science, like all past science, look so different to scientists and to historians? We should welcome the chance to engage such divergences as they arise in this bicentennial year of Darwin.

#### Bibliographical note

The textual, biographical and historiographical bases for what I have written here are given in this paper: ‘Darwin as a lifelong generation theorist’ [1]. That paper is reprinted without revisions, along with others on Darwin, in [2]. In that paper, I emphasised too much the integrations that Darwin was achieving by formulating pangenesis and natural selection as he did. In stressing, in the present paper, the paucity of those integrations, I may

have compensated a little too much for a past error. Two invaluable books should have been cited in that earlier paper: Gloria Robinson [3], and the monumental classic [4]. Wilson’s views about evolution, cytology and the potential unification of biology are expounded in the “Introduction” to his text on the cell. I have consulted the second edition [5]. Important recent studies of Darwin’s theory of pangenesis include: Ricardo Noguera-Solano and Rosaura Ruiz Gutiérrez [6]; the third chapter of Kyle Stanford’s book [7]; and Jim Endersby [8].

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