



Evolution / Évolution

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

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