Journal of the History of Biology **33:** 425–455, 2000.

Darwin on Variation and Heredity

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Abstract. Darwin's ideas on variation, heredity, and development differ significantly from twentieth-century views. First, Darwin held that environmental changes, acting either on the reproductive organs or the body, were necessary to generate variation. Second, heredity was a developmental, not a transmissional, process; variation was a change in the developmental process of change. An analysis of Darwin's elaboration and modification of these two positions from his early notebooks (1836–1844) to the last edition of the *Variation of Animals and Plants Under Domestication* (1875) complements previous Darwin scholarship on these issues. Included in this analysis is a description of the way Darwin employed the distinction between transmission and development, as well as the conceptual relationship he saw between heredity and variation. This paper is part of a larger project comparing commitments regarding variation during the latter half of the nineteenth century.

Keywords: Charles Darwin, development, externalism, generation, heredity, Pangenesis, nineteenth century, transmission, variation

On March 18, 1862, Darwin wrote a letter in reply to a communication from his botanist colleague J. D. Hooker. In this letter Darwin asserted:

> You speak of "an inherent tendency to vary wholly independent of physical conditions". This is a very simple way of putting the case (as Dr. Prosper Lucas also puts it); but two great classes of facts make me think that all variability is due to changes in the conditions of life. (1) that there is more variability & more monstrosities (& these graduate into each other) under unnatural domestic conditions, than under nature. And secondly that changed conditions affect in an especial manner the reproductive organs, – those organs which are to produce a new being.[1]

Darwin expressed his belief that "all variability is due to changes in the conditions of life." My paper explores the link Darwin saw between environments and organic variation.

[1] Burkhardt et al., 1997, p. 123.

Almost six years later, on February 28, 1868, Darwin wrote another letter to Hooker. Darwin had just presented his hypothesis of Pangenesis to the general public in the *Variation of Plants and Animals Under Domestication*, which was published on January 30, 1868.[2] In this letter, Darwin explained:

> 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.[3]

Darwin justified his "idea" of Pangenesis, which tied all aspects of variation, heredity, and development together. My paper also investigates Darwin's developmental views concerning both variation and heredity.

Evolutionary theory after the Modern Synthesis associates variation and its inheritance with internal causes such as mutation and the sequestered continuity of the germ-line. Evolutionary theory also links adaptation with external causes such as selection by the environment. Although Darwin's conception of the external sources of adaptation coincides with the modern position, his beliefs regarding variation and heredity differ from current theory in two crucial respects. First, Darwin held that environmental changes, acting either on the reproductive organs or the body, were absolutely necessary to generate variation. Second, heredity for Darwin was a developmental, not a transmissional, process. Variation occurred when the environment caused a change in the developmental process of change.

A complete and robust comprehension of Darwin's views on variation, heredity, and development requires a close analysis of Darwin's work from his early notebooks, started in 1836,[4] to the second edition of the *Variation of Animals and Plants Under Domestication*, published in 1875.[5] Furthermore, all the aspects of his position must be considered. Darwin scholarship

[2] Desmond and Moore, 1991, p. 550.
[3] Darwin, F., 1959, vol. II, p. 264.
[4] Barrett et al., 1987.
[5] Darwin, *Variation* (1875).

has tended to focus on blending inheritance and the issue of continuous vs. discontinuous variation.[6] My paper complements this work by analyzing Darwin's views on the external causes of variation and the developmental processes of both variation and heredity.

Darwin's Theory of External Causes of Heritable Variation

Throughout his career, Darwin consistently linked the cause of variation with changes in the environment; he was an externalist. Peter Godfrey-Smith defines externalism as explaining "properties of organic systems in terms of properties of their environments."[7] In discussing "the motor of organic change," Stephen J. Gould defines environmentalism as the belief that "the external environment and its alterations set the course of change."[8] I shall use the term "externalism." In contrast, an explanation is internalist if it explains properties of an organic system in terms of other properties of the organic system.[9] Gould explains internalism as the belief that "change[s] arise from some independent and internal dynamic within organisms themselves."[10] An externalist hypothesis explains insides using outsides; an internalist one explains insides using other insides.

Darwin held that the environment was necessary for both adaptation and variation. He provided an external mechanism for adaptation: natural selection. He also proposed an external mechanism for variation: changes in the environment. His views are part of a long tradition of externalist explanation in England. For instance, biologists who espoused either Natural Theology[11] or the common belief in the inheritance of acquired traits,[12] or both, were endorsing externalist explanations. Godfrey-Smith also discusses English externalism.[13] In this section I will trace, in a chronological fashion, the development of Darwin's externalist views on variation. For Darwin, as we shall see, all variation was potentially heritable in subsequent generations. *Therefore, the term variation in my paper will always refer to heritable variation.*

6 See Bowler, 1974; Geison, 1969; Ghiselin, 1969, Chapter 7, "Variation," pp. 160–186; Hull, 1973, "Fleeming Jenkin," pp. 302–350; Vorzimmer, 1963; Vorzimmer, 1970, Chapter 4, "The Causes of Variability," pp. 71–95.

7 Godfrey-Smith, 1996, p. 30.

8 Gould, 1977, p. 2.

9 Godfrey-Smith, 1996, p. 30.

10 Gould, 1977, p. 2.

11 Ospovat, 1981.

12 Zirkle, 1946.

13 Godfrey-Smith, 1996, pp. 43–44.

The following passage from *The Variation of Animals and Plants Under Domestication* (henceforth *The Variation of Animals and Plants*) epitomizes Darwin's strong externalist position on variation, "if it were possible to expose all the individuals of a species during many generations to absolutely uniform conditions of life, there would be no variability."[14]

Darwin's Early Views on Externally-caused Variations

As David Kohn shows, Darwin was thinking about transmutation writ large upon returning from his sea-faring voyage on the *Beagle*.[15] Darwin was in the process of developing a theory concerning the production of variation. The relationships between environment, sexual reproduction, variability, and adaptation drew his attention. In Notebook B (July 1837–March 1838)[16] he wrote, "The father being climatized, climatizes the child" (B90).[17] Here he suggested that change induced on the parent was hereditary. However, he noted that not all induced change was hereditary, for he asserted: "Any change suddenly acquired is with difficulty permanently transmitted" (B239).[18] In the notebooks, Darwin was unclear about the part of the organism affected by the external cause of variation. Concerning the relationship between induced variation and adaptation, Darwin thought that much variation was adaptive. He referred to "direct adaptation" (B46)[19] and also wrote, "What a magnificent view one can take of the world Astronomical <& unknown> causes, modified by unknown ones, cause changes in geography & changes of climate superadded to change of climate from physical causes. – these superinduce changes of form in the organic world, as adaptation" (D36, August 16, 1838).[20] Although this entry is somewhat unclear, it indicates that Darwin believed that change in the environment led directly to adaptive variation.

After reading Malthus in September 1838, Darwin found another means of explaining the existence of adaptation: natural selection. Variation was no longer necessarily adaptive. This shift in reasoning can be seen in Darwin's "wedge" entry in which he suggested that "The final cause of all this wedgings, must be to sort out proper structure and adapt it to change" (D135e, on or right after September 28, 1838).[21] The environment still

[14] Darwin, *Variation* (1868), II, p. 308; and Darwin, *Variation* (1875), II, p. 242. The two editions contain the same passage.

[15] Kohn, 1980.

[16] Barrett et al., 1987, p. 167.

[17] Ibid., 1987, p. 193.

[18] Ibid., 1987, p. 230.

[19] Ibid., 1987, p. 182.

[20] Ibid., 1987, pp. 342–343.

[21] Ibid., 1987, pp. 375–376.

caused most variation. Thus, Darwin's pattern of explanation was induced (not "spontaneous") variation, which was not necessarily adaptive, followed by environmental selection. Note that his and modern views agree on the overall pattern of variation occurring prior to selection.

Darwin's Basic Categories of Externally-caused Variations

In 1844 Darwin completed an essay which, among other ideas, contained his views on the origin of variation. Darwin attributed some variation to "the laws of embryonic growth and of reproduction."[22] But "the indirect effects of domestication on the action of the reproductive system" also caused variation.[23] This type of environmental action I will call *germinally-mediated*. He continued: "It would appear as if the reproductive powers failed in their ordinary function of producing new organic beings closely like their parents; and as if the entire organization of embryo, under domestication, became in a slight degree plastic."[24] Germinally-mediated variation was produced when the reproductive organs failed due to "considerable change from the natural conditions of life."[25] As Peter Bowler writes, "Darwin never gave up the belief that variations are caused when external conditions disturb the reproductive system."[26]

In the first edition (1859) of *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* (henceforth *On the Origin of Species*), Darwin reiterated his externalism. He wrote: "I am strongly inclined to suspect that the most frequent cause of variability may be attributed to the male and female reproductive elements having been affected prior to the act of conception. Several reasons make me believe in this; but the chief one is the remarkable effect which confinement or cultivation has on the functions of the reproductive system; this system appearing to be far more susceptible than any other part of the organisation, to the action of any change in the conditions of life."[27] Changes in the conditions of life triggered the reproductive organs to malfunction and to thereby produce variation.

In the first edition of *On the Origin of Species*, and to a lesser extent in the *Essay of 1844*, Darwin also held that the environment could produce variation in the body. This type of environmental action I will call *somatically-*

[22] Charles Darwin, *Essay of 1844* (1958), p. 95.
[23] Ibid., p. 96.
[24] Ibid., p. 96.
[25] Ibid., p. 96.
[26] Bowler, 1984, p. 161. See also Olby, 1966, pp. 55–62.
[27] Darwin, *Origin* (1859), p. 8.

mediated.[28] Darwin thought that the environment could produce little change through *direct*[29] action on the bodies of organisms, but through the *use and disuse* of organs, the environment could produce a fair amount of change.[30] Organisms could also become *acclimatized* to different climates, either through somatically-mediated changes in their habit or through "natural selection of varieties having different innate constitutions."[31] However, Darwin did not distinguish clearly between direct action and acclimatization by way of changes in habit. The former occurred through the action of "difference of climate, food, &c.,"[32] while the latter eventuated through the action of climate.[33] Since both happened as a result of differences in climate, and direct action was also caused by food, etc., the process of direct action seems to have included the process of acclimatization by way of changes in habit. However, acclimatization involved "habit"[34] whereas direct action did not. Darwin did not clearly explain the difference between the two. Whether there were two or three distinct environmental venues for somatically-mediated variation, it could all be inherited. In Chapter 1, "Variation under Domestication" of *On the Origin of Species*, Darwin wrote: "Perhaps the correct way of viewing the whole subject [of heredity], would be, to look at the inheritance of every character whatever as the rule, and non-inheritance as the anomaly."[35] Direct action, use and disuse, and acclimatization through changes in habit, represented different ways of acquiring characters, which were then often inherited.

In summary, Darwin considered two kinds of externally-induced variations: germinally-mediated and somatically-mediated. He called them, respectively, "indirect" and "direct."[36] The first was caused by the environment acting on the reproductive organs of the parent and causing variation in the *next* generation. Darwin called this effect "indirect" because the variation was caused in the generation prior to the generation that displayed it. The second refers to the environment acting on the body of an organism. He

[28] I am grateful to Peter Godfrey-Smith for suggesting this term.

[29] Darwin, *Origin* (1859), p. 132.

[30] Ibid., pp. 134–139.

[31] Ibid., p. 141.

[32] Ibid., p. 132.

[33] Ibid., pp. 139–143.

[34] Ibid., pp. 139–143.

[35] Ibid., p. 13. For further discussion on Darwin's views on the inheritance of variation see below, section II, E.

[36] He did this as early as his *Sketch of 1842*: Darwin, *Sketch of 1842* (1958), pp. 41–43. See also the 1869 and 1872 *Origin* where Darwin wrote, "changed conditions act in two ways, directly on the whole organisation or on certain parts alone [somatically-mediated], and indirectly through the reproductive system [germinally-mediated]" (Peckham, 1959, p. 276).

called this effect "direct" because the variation was caused and displayed in the *same* generation. "Mediated" refers to what parts (reproductive organs or body) link the effect of the environment to changes in the reproductive organs. Darwin did not propose a material mechanism for these two kinds of variations until his theory of Pangenesis in 1868 (see below, section "The Mechanics of Pangenesis").

Two Internal Mechanisms for Variation

In addition to these external mechanisms, Darwin also suggested two internal mechanisms for variation. Early in his career Darwin proposed that, "[a] certain degree of variation (Müller's twins) seems inevitable effect of process of reproduction."[37] Crossing encompassed two internal causes of variation: (1) crossing between organisms of the same variety and (2) crossing between organisms of different varieties or species. Darwin vaguely mentioned the first, intra-variety crossing, as a cause of variation twice (both on page 10) in *On the Origin of Species* (1859); he did not mention it at all in Chapter 5, "Laws of Variation." In the last edition (1872) of *On the Origin of Species*, as well as in both editions of *The Variation of Animals and Plants*, he dropped this explanation as a cause of variation.

Darwin discussed the second, crossing of two individuals of different varieties or species, as a cause of variation in "Hybridism," Chapter 8 of *On the Origin of Species* (1859):

> The slight degree of variability in hybrids from the first cross or in the first generation, in contrast with their extreme variability in the succeeding generations, is a curious fact and deserves attention. For it bears on and corroborates the view which I have taken on the cause of ordinary variability; namely, that it is due to the reproductive system being eminently sensitive to any change in the conditions of life, being thus often rendered either impotent or at least incapable of its proper function of producing offspring identical with the parent-form. Now hybrids in the first generation are descended from species (excluding those long cultivated) which have not had their reproductive systems in any way affected, and they are not variable; but hybrids themselves have their reproductive systems seriously affected, and their descendants are highly variable.[38]

The reproductive organs can be affected either by the cross-breeding of distinct varieties or species, or by changes in the conditions of life. In both cases, the causal explanation for variation involved altered reproductive

[37] Darwin, *Sketch of 1842* (1958), p. 41.
[38] Darwin, *Origin* (1859), p. 273.

systems. This was the *only* internal reason for variation that Darwin consistently allowed throughout his career, but he did not utilize it often. In *The Variation of Animal and Plants*, Darwin noted: "Although we have not at present sufficient evidence that the crossing of species, which have never been cultivated, leads to the appearance of new characters, this apparently does occur with species which have been already rendered in some degree variable through cultivation."[39] Thus, Darwin came to believe that hybrids would become variable when their reproductive organs were already exposed to changes in the conditions of life. In this way, Darwin made his only internal mechanism for variation, hybridization, dependent on environmental changes.

Darwin's Externalism Solidified

Darwin's externalism became more explicit in *The Variation of Animals and Plants*. In responding to beliefs that variation was "necessar[ily] contingent on reproduction" or that it depended "exclusively on the crossing of primordially distinct forms," Darwin explained, "we must, I think, take a broader view, and conclude that organic beings, when subjected during several generations to any change whatever in their conditions, tend to vary; the kind of variation which ensues depending in most cases in a far higher degree on the nature or constitution of the being, than on the nature of the changed conditions."[40] Although the kind of variation depended more on the nature of the organism than on the nature of the conditions of life, changes in the conditions of life triggered variation. Darwin introduced the distinction between the nature of the organism and the nature of the environment in the first edition (1868) of *The Variation of Animals and Plants* and the fifth edition (1869) of *On the Origin of Species* in part because of his own conclusions and in part because of August Weismann's work.[41] At the end of Chapter 22, "Causes

[39] Darwin, *Variation* (1875), II, p. 254. See also *Variation* (1868), II, p. 319 for a similar passage.

[40] Darwin, *Variation* (1875), II, p. 237. See also Darwin, *Variation* (1868), II, p. 303. The only difference between the passages in the two editions is the absence of the phrase "in most cases" in the 1868 edition.

[41] Weismann was mentioned in both the 1869 and 1872 *Origin*: "With respect to the direct action [somatically-mediated], we must bear in mind that in every case, as Professor Weismann has lately insisted, and as I have incidentally shown in my work on 'Variation under Domestication,' there are two factors: namely, the nature of the organism, and the nature of the conditions" (Peckham, 1959, p. 78). See also Darwin, *Variation* (1868), II, pp. 351–352 and Darwin, *Variation* (1875), II, p. 282. Of the two editions, Weismann was mentioned only in the *Variation* (1875). Presumably Darwin read something relevant by Weismann sometime in 1868 or 1869. Perhaps he received the "kleine Schrift", which was Weismann's *Über die Berechtigung der Darwin'schen Theorie* (1868). That piece had not yet arrived in the post when Darwin wrote to Weismann on October 22, 1868; it might have arrived at a later

of Variability", Darwin wrote: "We are thus driven to conclude that in most cases the conditions of life play a subordinate part in causing any particular modification; like that which a spark plays, when a mass of combustibles bursts into flame – the nature of the flame depending on the combustible matter, and not on the spark."[42] Although he was internalist when considering the *nature* of each particular variation, he held an explicitly externalist view of the *triggering cause* for each particular variation.

In the conclusion to *The Variation of Animals and Plants*, Darwin tied his internalist position on the nature of each variation with his externalist perspective of the triggering cause for each variation. He asserted: "Although *every* variation is either directly [somatically-mediated] or indirectly [germinally-mediated] caused by some change in the surrounding conditions, we must never forget that the nature of the organisation which is acted on, is by far the more important factor in the result. We see this in different organisms, which when placed under similar conditions vary in a different manner, whilst closely-allied organisms under dissimilar conditions often vary in nearly the same manner."[43]

The strongest example of Darwin's externalism appeared in both editions of *The Variation of Animals and Plants*: "These several considerations alone render it probable that variability of every kind is directly [somatically-mediated] or indirectly [germinally-mediated] caused by changed conditions of life. Or, to put the case under another point of view, *if it were possible to expose all the individuals of a species during many generations to absolutely uniform conditions of life, there would be no variability*."[44] Darwin noted that with "absolutely uniform conditions of life, there would be no variability." Or conversely, if there was variability, the organisms would have necessarily been exposed to changes in the conditions of life. Darwin presented two qualifiers in this passage: "all the individuals of a species" and "during many generations." The reason for the first was that if just one organism

date (see Darwin, F., 1903, I, pp. 310–311). This is the first known letter from Darwin to Weismann (Frederick Churchill, pers. com.). Alternatively, one of Weismann's letters could have contained some relevant argument. However, we do not have any records of letters from Weismann to Darwin (Frederick Churchill, pers. com.).

[42] Darwin, *Variation* (1868), II, pp. 351–352 and Darwin, *Variation* (1875), II, p. 282. The two editions contained the same passage. In the 1875 edition, however, there was a footnote to Weismann's 1875 article entitled "Saison-Dimorphismus der Schmetterlinge." Darwin explained that Weismann "argues strongly in favour of this view." This footnote was absent in the 1868 edition. Weismann's article appeared in translation in 1882; Darwin wrote a "prefatory notice" to this collection of articles (Weismann, 1882).

[43] Darwin, *Variation* (1875), II, p. 415 (emphasis mine). See *Variation* (1868), II, p. 502 for a similar passage.

[44] Darwin, *Variation* (1868), II, p. 308 and Darwin, *Variation* (1875), II, p. 242 (emphasis mine). The two editions contain the same passage. The passage is found at the beginning of Chapter 22.

was exposed to changes in the conditions of life, it could vary and introduce this variation into the population. The reason for the second was "that when the organisation has once begun to vary, it generally continues to vary for many generations."[45] Thus there would be a lag time of several generations between the presence of uniform conditions of life and the complete ceasing of variation in every individual. These qualifiers did not weaken Darwin's main claim. Variability was necessarily tied with changes in the conditions of life.

In a passage that appears a scant two pages before, Darwin noted, "[w]e will now consider the general arguments, which appear to me to have great weight, in favour of the view that variations of all kinds and degrees are directly [somatically-mediated] or indirectly [germinally-mediated] caused by the conditions of life to which each being, and more especially its ancestors, have been exposed."[46] The view to which Darwin was referring was his own. Changes in the conditions of life were necessary to induce variation. However, Darwin nowhere implied that given changes in the conditions of life, variation must occur. Changes in the conditions of life may or may not lead to variation. Uniform conditions of life did not lead to variation.[47]

This was not to say that with uniform conditions of life there was no variation in the form of blending or reversion. But no new variability was introduced. Darwin distinguished new variability from other forms of variability in the same book: "The dissimilarity of brothers or sisters of the same family, and of seedlings from the same capsule, may be in part accounted for by the *unequal blending* of the characters of the two parents, and by the more or less complete recovery through *reversion of ancestral characters* on either side; but we thus only push the difficulty further back in time, for what made the parents or their progenitors different?"[48] Some cause must have originally produced the differences. Changes in the conditions of life *ultimately* caused all genuinely new variation; reversion and blending exemplified the rearrangement of already existing-variation.[49]

[45] Peckham, 1959, p. 78. This passage remained intact throughout all six editions, except for an inserted comma in the 4th edition.

[46] Darwin, *Variation*, (1868), II, p. 306 and Darwin, *Variation*, (1875), II, pp. 240–241. The two editions contain the same passage.

[47] To use the language of formal logic, Darwin's position can be translated as: "if variation, then changes in the conditions of life." This is a conditional, *not* a biconditional. Therefore this claim is specifically *not* equivalent to "if changes in the conditions of life, then variation."

[48] Darwin, *Variation* (1868), II, p. 304 and Darwin, *Variation* (1875), II, p. 239 (emphasis mine). The two editions contain the same passage.

[49] In the fifth chapter of the *Origin* (1859), Darwin also listed "correlation of growth" and "law of compensation" as laws of variation. But these internal mechanisms were really

An examination of a specific problem, which concerned Darwin throughout his career, will exemplify his increased externalism. Darwin wondered why seeds that developed in the same capsule on the same plant developed into different adults. They came from the same parents and were exposed to the same conditions of life – why should they then have varied?

In the *Essay of 1844*, Darwin claimed that the variation of the seeds must be attributed "to the laws of embryonic growth and of reproduction," since the seeds have "matured in the very same capsule, with the male and female principle nourished from the same roots and *necessarily exposed to the same external influences*."[50] In *On the Origin of Species* (1859), Darwin wrote that the seeds "have *apparently* been exposed to exactly the same conditions of life."[51] He also did not dismiss the conditions of life as a cause of variability in this case. He merely claimed that they were "unimportant . . . in comparison with the laws of reproduction, and of growth, and of inheritance."[52] In *The Variation of Animals and Plants*, however, Darwin attributed the variation to changes in the conditions of life. He explained, "the belief that an innate tendency to vary exists, independently of external conditions, seems at first sight probable. But even the seeds nurtured in the same capsule *are not subjected to absolutely uniform conditions*, as they draw their nourishment from different points; and we shall see in a future chapter that this difference sometimes suffices greatly to affect the character of the future plant."[53] By 1868 Darwin explained the seed variation in terms of changing conditions. These arguments all concern the introduction of new variation, not the rearrangement of already-existing variation.

Darwin shifted from the view, stated in the *Essay of 1844*, that seeds were exposed to exactly the same conditions to the belief, formulated in *The Variation of Animals and Plants*, that seeds were exposed to changing conditions. In *The Variation of Animals and Plants* Darwin solidified his externalism with respect to the causes of variation.

secondary causes of variation (see Vorzimmer, 1970, pp. 71–95). Changes in the conditions induced variation upon which other variation was correlated. Again, changes in the conditions of life were the *ultimate* source of variation.

[50] Darwin, *Essay of 1844* (1958), p. 95 (emphasis mine).

[51] Darwin, *Origin* (1859), p. 10 (emphasis mine).

[52] Darwin, *Origin* (1859), p. 10.

[53] Darwin, *Variation* (1868), II, pp. 304–305 (emphasis mine). See also Darwin, *Variation* (1875), II, p. 239. The only difference between the passages in the two editions is that "external differences" is substituted for "external conditions," and "greatly" was omitted in the 1875 edition.

What are "Changes in the Conditions of Life"?

Darwin repeatedly stressed that it was "changes in the conditions of life," not just the "conditions of life," that triggered variation. What differentiated the former from the latter?

Almost all environments experience fluctuations in temperature, humidity, light, chemical composition, etc. Did Darwin include these fluctuations as one set of the conditions of life – thereby implying that the changes in the conditions of life were changes in patterns of fluctuations, or did he think that fluctuations themselves constituted changes in the conditions of life? Darwin was vague on this point. He admitted that "[i]n a confined or isolated area, if not very large, the organic and inorganic conditions of life will generally be in a great degree uniform."[54] Clearly the area included fluctuations and since he called this area uniform in terms of its conditions of life, Darwin must have meant that a single kind of condition of life included fluctuations. On the other hand, Darwin also wrote: "But even the seeds nurtured in the same capsule are not subjected to absolutely uniform conditions, as they draw their nourishment from different points."[55] Fluctuating conditions were here considered different conditions (of life). With this understanding of the conditions of life, variation would be more prevalent than with the former conception, since any fluctuation would count as a changing condition. Darwin did not explicitly define the conditions of life, probably because he neither classified nor theorized about the properties of environments (e.g. complexity, heterogeneity, and type). Despite his vagueness, Darwin consistently claimed that *changes in the conditions of life*, whatever they exactly are, triggered variation.

The Shift in Emphasis from Germinally-mediated to Somatically-mediated Variations

In part because of Jenkin's 1867 criticism of blending inheritance and in part because of his own developing views on heredity, Darwin thought that rare variations would generally blend out and be lost in a population.[56] Furthermore, since the Earth was "proved," in the early 1860s, to be young by William Thomson (later titled Lord Kelvin), there was not enough time for evolution to occur if selection relied solely on variations which were random with respect to adaptive direction; evolution needed to be acceler-

[54] Darwin, *Origin* (1859), p. 104. In both the 1869 and 1872 editions, Darwin replaced "in a great degree" with "almost" (Peckham, 1959, p. 196).

[55] Darwin, *Variation* (1868), II, p. 305 and Darwin, *Variation* (1875), II, p. 239. The two editions contain the same passage.

[56] For scholarship addressing these issues see above, n. 6.

ated.[57] For these reasons among others, Darwin increasingly required the existence of both systematic and necessarily adaptive variations. Darwin divided variation into "definite" and "indefinite", which I call systematic and unsystematic.[58] Definite variation occurred "when all or nearly all the offspring of individuals exposed to certain conditions during several generations are modified in the same manner."[59] Indefinite variation occurred when a changed condition of life "cause[d] one individual to vary in one way and another individual in another way."[60] *Germinally-mediated variations were neither systematic ("definite") nor necessarily adaptive; somatically-mediated variations sometimes were one or the other or both.* Systematic somatically-mediated variations did not blend out of the population since many variations of the same type occurred; necessarily adaptive somatically-mediated variations sped up evolution since the "right" variation necessarily occurred. Darwin shifted emphasis from germinally-mediated to systematic and necessarily adaptive somatically-mediated variations in the late 1860's in order to both avoid the problem of blending and to speed up evolution.

Two sets of parallel passages from *On the Origin of Species* display this change in emphasis.

First passage from the first (1859) edition:

> In looking at many small points of difference between species, which, as far as our ignorance permits us to judge, seem to be quite unimportant, we must not forget that climate, food, &c., *probably produce some slight and direct effect.*[61]

[57] This claim is problematic. Although Darwin did not believe Thomson's calculations, they convinced many, including Wallace. Darwin could no longer, in published works, assume multiple hundreds of millions of years when Thomson placed an upper limit of 100 million years since the condensation of the Earth's crust. While rejecting this estimate, Darwin had to accept it in published work. To Hooker Darwin, on July 24, 1869, wrote, "I am glad I have faced and admitted the difficulty [regarding Thomson's calculations of the age of the Earth] in the last [fifth] edition of the *Origin* . . ." (Darwin, F., 1903, I, p. 314). For the purposes of my paper, I focus on Darwin's published views. For further discussion and references see Bowler, 1984; Burchfield, 1990; Desmond and Moore, 1991, Chapter 38; Hull, 1973, pp. 302–350.

[58] He did this as early as the *Sketch of 1842* (1958), p. 44 although he did not stress the distinction until the fifth edition of *On the Origin of Species* (Peckham, 1959, p. 78). This distinction is orthogonal to the direct/indirect distinction.

[59] Peckham, 1959, p. 78 (passage found in 1869 and 1872 *Origin*). Similar passages are found in Darwin, *Variation* (1868), II, pp. 327–328 and Darwin, *Variation* (1875), II, p. 260.

[60] Darwin, *Variation* (1875), II, p. 260. The 1869 and 1872 *Origin* contain a similar passage (Peckham, 1959, pp. 78–79). In the 1868 edition of the *Variation*, Darwin did not explain indefinite variation.

[61] Darwin, *Origin* (1859), p. 85 (emphasis mine); Peckham, 1959, pp. 170–171.

From the sixth (1872) edition:

> In looking at many small points of difference between species, which, as far as our ignorance permits us to judge, seem quite unimportant, we must not forget that climate, food, &c., *have no doubt produced some direct effect*.[62]

Second passage from the first (1859) edition:

> How much direct effect difference of climate, food, &c., produces on any being is extremely doubtful. My impression is, that the effect is *extremely small* in the case of animals, but *perhaps* rather more in that of plants.[63]

From the sixth (1872) edition:

> It is very difficult to decide how far changed conditions, such as of climate, food, &c., have acted in a definite [systematic] manner. There is reason to believe that in the course of time the effects have been *greater* than can be *proved* by clear evidence.[64]

In 1859 germinally-mediated variations accounted for almost all variation; by 1872 somatically-mediated variations accounted for much variation.[65]

The fact that in both the 1869 and 1872 editions Darwin deleted sentences indicating that germinally-mediated variations were the "most frequent cause

[62] Peckham, 1959, pp. 170–171 (emphasis mine).

[63] Darwin, *Origin* (1859), p. 132 (emphasis mine); Peckham, 1959, p. 276.

[64] Peckham, 1959, pp. 276–277 (emphasis mine).

[65] Ibid., pp. 276–277, traces the change in the second sentence of the second passage.
1859 (1st edn.): My impression is, that the effect is extremely small in the case of animals, but perhaps rather more in that of plants.
1861 (3rd edn.): My impression is, that the effect is small in the case of animals, but more in that of plants. ["Extremely" and "perhaps rather" are removed.]
1869 (5th edn.): There is some reason to believe that in the course of time the effects have been greater than can be proved to be the case by any clear evidence. [*Ad hoc* statement: there is no data for this claim.]
1872 (6th edn.): There is reason to believe that in the course of time the effects have been greater than can be proved by clear evidence. ["Some," "to be the case," and "any" are omitted.]
These changes reveal a Darwin who, otherwise so careful with facts, significantly increased the importance of somatically-mediated effects by making *ad hoc* changes to his text that were not warranted factually.
In the fifth edition, Darwin replaced "direct" with "definite" in the first sentence of the second set (Peckham, 1959, p. 276). Therefore, the above comparison of the six editions is less useful than if "direct" were present throughout. However, Darwin did believe that only somatically-mediated variation could be "definite" (systematic), so when he wrote "definite," he also implied "direct."

of variability" also illustrate his change in emphasis.[66] During his career he did not change his views on the quantity of variation in nature and under domestication, but he changed his beliefs regarding the relative frequency of somatically-mediated as compared to germinally-mediated variations.

This shift produced a problem for Darwin. As he felt that a larger proportion of the variations induced by the environment were adaptive, the relative importance of selection in the production of adaptation diminished. In a letter to Asa Gray dated May 8, 1868, Darwin expressed the problem clearly: "If the right variations occurred, and no others, natural selection would be superfluous."[67] Due to its logical nature, the problem was unsolvable.

In *The Variation of Animals and Plants* (1868) Darwin still championed the importance of natural selection,

> We must not exaggerate the importance of the definite action of changed conditions in modifying all the individuals of the same species in the same manner, or of use and disuse. As every part of the organisation is highly variable, and as variations are so easily selected, both consciously and unconsciously, it is very difficult to distinguish between the effects of the *selection of indefinite variations*, and the *direct action of the conditions of life*. For instance, it is possible that the feet of our waterdogs, and of the American dogs which have to travel much over the snow, may have become partially webbed from the stimulus of widely extending their toes; but it is *far more probable* that the webbing, like the membrane between the toes of certain pigeons, spontaneously appeared and was afterwards increased by the best swimmers and the best snow-travellers being preserved during many generations.[68]

Direct and definite somatically-mediated variations were less important than the selection of indefinite (unsystematic) variations. Although *The Variation of Animals and Plants* (1875) contains a similar passage, the differences are worth noting because they show Darwin's increased commitment to systematic and necessarily adaptive somatically-mediated variations. The first sentence was omitted in the second edition as if to allow him to "exaggerate the importance" of somatically-mediated variations. Furthermore, the second sentence was rewritten: "As *almost* every part of the organisation *becomes* highly variable *under domestication*, and as variations are [CD omits "so"]

[66] Peckham, 1959, pp. 79–80 and p. 276.

[67] Darwin, F., 1959, II, pp. 267.

[68] Darwin, *Variation* (1868), II, pp. 500–501 (emphasis mine). Darwin was thinking of this specific example as early as Notebook E. He wrote: "Are the feet of water-dogs at all more webbed than those of other dogs – if nature had had the picking she would make <them> such a variety far more easily than man" (E63, on or right after December 2, 1838) (Barrett et al., 1987, p. 414).

easily selected both consciously and unconsciously . . . but it is [CD omits "far"] more probable . . ."[69] The first three changes (indicated by emphases) demonstrate Darwin's increased knowledge concerning the constraints on variation that organisms manifested under domestication; these changes do not provide exegetical information concerning the relative importance of selection vs. direct action. The last two omissions do provide such information: variations were not "so" easily selected, and it was no longer "far" more probable that selection as opposed to direct action accounted for the webbing of waterdog feet. Thus, these two omissions together with the omission of the whole first sentence in *The Variation of Animals and Plants* (1875), indicate that Darwin increasingly emphasized the importance of somatically-mediated variations in explaining the production of adaptations. Despite his change in emphasis, however, Darwin continued to believe that "Natural Selection has been the most important, but not the exclusive, means of modification."[70]

Darwin was caught in the logical bind he had communicated to Asa Gray. He attempted to champion the importance of natural selection in producing adaptations while also accentuating systematic and necessarily adaptive somatically-mediated variations. Although emphasizing one source of adaptation necessarily decreased the importance of the other, Darwin, in his published works, inconsistently stressed both.

In summary, Darwin's work from 1837 to 1875 presents three main shifts in his views on the external causes of variation. First, he became more explicit about the absolute necessity of changes in the conditions of life for variation, culminating in 1868 with the statement, "[with] absolutely uniform conditions of life, there would be no variability" (above, n. 44). Second, while stressing the necessity of changes in the conditions of life for triggering variation, he viewed the nature of the organism as more important than the nature of the changed conditions in determining the nature of the variation. Third, he increasingly emphasized somatically-mediated variations at the expense of germinally-mediated variations in order to view a larger proportion of variation as systematic and necessarily adaptive.

We need to call Darwin an externalist when considering the *triggering cause* of variation, since he consistently emphasized environmental changes. We need to identify Darwin as an internalist when dealing with the *nature* of variation, since he prioritized the nature of the organism. It is clear that in either case we cannot call him an "interactionist," which would imply that he explained the triggering cause or the nature of variation in terms of interactions between the organism and the environment. Furthermore, since he distinguished and did not link the triggering cause with the nature of vari-

[69] Darwin, *Variation* (1875), II, pp. 414–415 (emphasis mine).
[70] Peckham, 1959, p. 75.

ation, he cannot be considered an interactionist in this way either. For the purposes of my paper it is therefore not important to discuss further what an interactionist theory would entail.[71]

Darwin's Pangenesis: A Developmental Theory of Heredity

Thus far I have shown that Darwin theorized about the causes of variation from early on in his career. Now I want to emphasize that included in this theorization was his concern with development or what he called "generation." This concern was central to his theory of heredity, which linked external causes of variation with the development and transmission of variation.

Darwin's Early Concerns with Development

As M. J. S. Hodge shows, Darwin was a "lifelong generation theorist."[72] Hodge traces the development in private notebooks of Darwin's "identity thesis", which was that sexual reproduction, asexual reproduction, and regeneration were all particular instantiations of a general phenomenon: growth (and division).[73] Furthermore, Hodge notes that this growth or generation, "is in, of and by itself perfectly conservative."[74] Thus, in 1837, Darwin already had the seeds for a developmental theory of heredity: generation is conservative unless enacted upon by changes in the environment.

But it was not just in Darwin's early notebooks or in his later work on variation under domestication that we see this theory of heredity. For instance, in *On the Origin of Species* (1859) he wrote: "When a character which has been lost in a breed, reappears after a great number of generations, the most probable hypothesis is, not that the offspring suddenly takes after an ancestor some hundred generations distant, but that in each successive generation there has been a tendency to reproduce the character in question, which at last, under unknown favourable conditions, gains an ascendancy."[75] In this passage he referred to "a tendency to reproduce the character", which constituted a developmental tendency. He made this explicit in both the 1869 and 1872 editions of *On the Origin of Species* where he substituted "is developed" for "gains an ascendancy."[76] In *On the Origin of Species* (1859), Darwin also

[71] For more discussion on interactionist theories see Griesemer, 1993; Griesemer, in prep.; Levins and Lewontin, 1985; Oyama, 1985.

[72] Hodge, 1985.

[73] Hodge, 1985, pp. 213, 218–219.

[74] Hodge, 1985, p. 219.

[75] Darwin, *Origin* (1859), pp. 160–161.

[76] Peckham, 1959, p. 310. In the fifth edition of the *Origin*, Darwin also wrote: "The possibility of characters long lying latent can be understood according to the hypothesis of

had a principle that "at whatever period of life a peculiarity first appears, it tends to appear in the offspring at a corresponding age, though sometimes earlier."[77] These quotations, together with the section entitled "Embryology" in Chapter 13, indicate Darwin's concern with development in *On the Origin of Species* (1859).[78]

Cause vs. Display of a Variation

In *On the Origin of Species* (1859), Darwin also introduced an important distinction, which he used for the remainder of his career. In the section on "Embryology", he explained: "The question [of when a variation appears] is not, at what period of life any variation has been *caused*, but at what period it is fully *displayed*. The cause may have acted, and I believe generally has acted, even before the embryo is formed; and the variation may be due to the male and female sexual elements having been affected by the conditions to which either parent, or their ancestors, have been exposed."[79] Darwin claimed that many variations were *caused* in the parental generation independently of any *display* in the parental generation; these were the germinally-mediated variations. By discussing this type of variation, Darwin introduced a novel explanation for variation. Darwin also held that some variations were both caused and displayed in the parental generation; these were the somatically-mediated variations. The distinction between cause and display of variation indicates that Darwin was concerned with both the timing and location of environmental effects during the development of an organism.

The Mechanics of Pangenesis

By way of introducing Pangenesis, let us examine a passage from the *Essay of 1844* in which Darwin wrote: "From the following peculiarities of structure being inheritable and appearing only when the animal is full-grown – namely, general size, . . . change of colour in hair and its loss; deposition of bony matter on the legs of horses; blindness and deafness . . . etc.; from all such tendencies being I repeat inheritable, we clearly see that the germinal vesicle is impressed with some power which is wonderfully preserved during the production of infinitely numerous cells in the ever changing tissues, till

pangenesis, which I have given in another work" (Peckham, 1959, p. 310). This passage was removed in the sixth edition.

[77] Darwin, *Origin* (1859), p. 13; see also p. 444.

[78] Richards (1992), shows, in great detail, Darwin's concern with development in the 1859 *Origin* and earlier.

[79] Darwin, *Origin* (1859), p. 443 (emphasis mine). The 1869 and 1872 *Origin* (Peckham, 1959, p. 692) contain a similar passage.

the part ultimately to be affected is formed and the time of life arrived at."[80] Darwin stated that the germinal vesicle was "impressed with some power" that accounted for the expression of similarities between parents and offspring. Darwin was aware of the problem of differentiation in development. Different kinds of cells have different characters; the "power" that caused a character later in development had to wait for the right location and time. Furthermore, in this passage he mentioned the causal link from germ vesicle to adult body but not vice-versa.

Twenty-four years after Darwin completed this essay, the first edition of *The Variation of Animals and Plants* appeared. In this work he proposed his "Provisional Hypothesis of Pangenesis" (Chapter 27). His hypothetical heritable elements, the gemmules, were the physical carriers of the "power" that caused the expression of the characters inherited from the parents. Whereas in the *Essay of 1844* he wrote about abstract "power[s]" that determined heritable characters, in *The Variation of Animals and Plants* he postulated material gemmules that embodied these "powers[s]." Furthermore, with Pangenesis, Darwin discussed both the causal links from germ vesicle to adult body and vice-versa.

Darwin found that he "ha[d] been led, or rather forced, to form a view which to a certain extent connects these facts by a tangible method."[81] "These facts" were "those [which] [bear] on bud-variation, the various forms of inheritance, [and] the causes and laws of variation."[82] This "method" or "view" was "the hypothesis of Pangenesis, which implies that the whole organisation, in the sense of every separate atom or unit, reproduces itself. Hence ovules and pollen grains, – the fertilised seed or egg, as well as buds, – include and consist of a multitude of germs thrown off from each separate atom of the organism."[83] The growth of the gemmules accounted for phenomena as divergent as regular growth and differentiation, repair of injuries, and asexual and sexual reproduction.[84] Pangenesis concerned the mechanics of development.

More detail on Pangenesis is in order. In the second, theoretical part of the chapter on Pangenesis, Darwin asserted:

[80] Darwin, *Essay of 1844* (1958), pp. 226–227.

[81] Darwin, *Variation*, (1868), II, p. 428 and Darwin, *Variation* (1875), II, p. 349. The two editions contain the same passage.

[82] Darwin, *Variation*, (1868), II, p. 428 and Darwin, *Variation* (1875), II, p. 349. The two editions contain the same passage.

[83] Darwin, *Variation* (1868), II, p. 429. Darwin, *Variation* (1875), II, p. 350 contains a similar passage, but the first "atom" was omitted and the second "atom" was replaced by "part or unit" (see below, notes 96 and 119).

[84] Darwin, *Variation* (1868), II, pp. 433–434 and Darwin, *Variation* (1875), II, p. 357. The word choice is different in each edition, but both editions list the same kinds of phenomena.

> It is almost universally admitted that cells, or the units of the body, propagate themselves by self-division or proliferation, retaining the same nature, and ultimately becoming converted into the various tissues and substances of the body. But besides this means of increase I assume that cells, before their conversion into completely passive or "form-material," throw off minute granules or atoms, which circulate freely throughout the system, and when supplied with proper nutriment multiply by self-division, subsequently becoming developed into cells like those from which they were derived. These granules for the sake of distinctness may be called cell-gemmules, or, as the cellular theory is not fully established, simply gemmules. They are supposed to be transmitted from the parents to the offspring, and are generally developed in the generation which immediately succeeds, but are often transmitted in a dormant state during many generations and are then developed. Their development is supposed to depend on their union with other partially developed cells or gemmules which precede them in the regular course of growth. Why I use the term union, will be seen when we discuss the direct action of pollen on the tissues of the mother-plant. Gemmules are supposed to be thrown off by every cell or unit, not only during the adult state, but during all the stages of development. Lastly, I assume that the gemmules in their dormant state have a mutual affinity for each other, leading to their aggregation either into buds or into the sexual elements. Hence, speaking strictly, it is not the reproductive elements, nor the buds, which generate new organisms, but the cells themselves throughout the body. These assumptions constitute the provisional hypothesis which I have called Pangenesis.[85]

Every part of the body threw off gemmules at various developmental stages. The reproductive organs collected these gemmules to form the sperm or the egg.[86] The development of an organism depended on the union of the inher-

[85] Darwin, *Variation* (1868), II, pp. 448–449. Darwin, *Variation* (1875), II, pp. 369–370 contains a similar passage which we shall examine below. In 1865 Darwin completed a Pangenesis manuscript, which remained unpublished during his life (see Olby, 1963). Darwin developed the ideas presented in this manuscript in *The Variation of Animals and Plants*.

[86] It is interesting that Darwin did briefly consider asexual forms of reproduction such as fission (which he called "fissiparous generation", Darwin, *Variation* (1868), II, p. 429–431 and Darwin, *Variation* (1875), II, p. 351–352) in the beginning of the chapter on Pangenesis, but focused almost exclusively on sexual reproduction for the remainder of the chapter. Despite this focus, Darwin did not explicitly consider much of the literature on the physiology of the reproductive organs. He did outline experiments to answer some of these concerns in his "Questions and Experiments" (see Barrett et al., 1987, pp. 487–516). For example, he wrote: "(3) Sow seeds and place cuttings or bulbs in several different soils & temperatures & see what the effect will be – will seedlings vary much more than cuttings &c" (Barrett et al., 1987, p. 495). But his "Questions and Experiments" was concerned more with observa-

ited gemmules, from various life stages of the parent, with developing cells or gemmules in the organism's body. These developing cells were themselves products of gemmules that were activated upon contact either "with pre-existing nascent cells in due order of succession"[87] or with other gemmules. Concerning the regeneration of a tadpole tail, Darwin noted, "gemmules of all the units which compose the tail are diffused throughout the body at all ages. But during the adult state the gemmules of the larval tail would remain dormant, for they would not meet with pre-existing cells in a proper state of development with which to unite."[88] Gemmules were produced either by the relevant part (e.g. eye, liver, etc.) or by self-division. Some gemmules also persisted in a latent form. Darwin used an analogy: "The retention of free and undeveloped gemmules in the same body from early youth to old age will appear improbable, but we should remember how long seeds lie dormant in the earth and buds in the bark of a tree."[89] Whether a gemmule was activated or lay dormant depended on the "proper conditions."[90] These conditions included internal factors such as the organism being an outcome of a "cross" as well as external factors such as "[a] return . . . of domesticated animals and cultivated plants to a wild state."[91] The activation of a gemmule, which is known as reversion when the gemmule in question is latent in immediate ancestors, did not count as a new variation (see the passage of n. 48 above).

Two differences between the lengthy passage quoted above in *The Variation of Animals and Plants* (1868) and the 1875 edition are worth noting. First, in the 1875 passage the phrase "but not necessarily during the continued existence of the same unit" was appended to the sentence beginning "Gemmules are supposed to be thrown off by every cell or unit . . . "[92] Darwin probably added this as a clarification of his 1869 response to a short published piece by the Italian botanist Federico Delpino criticizing Pangen-

tion of patterns of variation than with experimentation on physiological mechanisms of the reproductive organs. Presumably, the latter would have been of great importance to him in articulating Pangenesis.

87 Darwin, *Variation* (1875), II, p. 371. See also Darwin, *Variation* (1868), II, p. 451 for a similar passage.

88 Darwin, *Variation* (1868), II, p. 451. Darwin omitted these sentences from the 1875 *Variation*, probably as a consequence of Federico Delpino's criticisms to be discussed below.

89 Darwin, *Variation* (1868), II, p. 453 and Darwin, *Variation* (1875), II, p. 373. The two editions contain the same passage.

90 Darwin, *Variation* (1868), II, p. 447 and Darwin, *Variation* (1875), II, p. 369. The two editions contain the same passage.

91 Darwin, *Variation* (1875), II, p. 59. Darwin, *Variation* (1868), II, pp. 105–106 contains a similar passage regarding these conditions.

92 Darwin, *Variation* (1875), p. 370.

esis.[93] Delpino had stated that Pangenesis required that all cells continually throw off gemmules. Darwin could "see no such necessity."[94]

Second, in the 1875 passage the reference to "the cellular theory" was removed. Pangenesis was inconsistent with the newer cellular theory of Rudolph Virchow, which claimed that all cells must be derived from other cells.[95] In Pangenesis, gemmules, which were all sub-cellular, gave rise to new cells either by uniting with other cells or gemmules. Even when sub-cellular gemmules united with cells to make more cells, the doctrine of all cells originating from other cells was contradicted. Darwin was aware of the difficulty of his position *vis-à-vis* the newer cellular theory. In discussing the differences between the newer cellular theory and the older views that cells arose from sub-cellular materials he wrote: "As I have not especially attended to histology, it would be presumptuous in me to express an opinion on the two opposed doctrines [(1) cells must be derived from other cells (Virchow) or (2) cells can arise from sub-cellular materials]. But every one appears to admit that the body consists of a multitude of "organic units," [here he cites a proponent of the view that sub-cellular materials can give rise to cells] each of which possesses its own proper attributes, and is to a certain extent independent of all others. Hence it will be convenient to use indifferently the terms cells or organic units or simply units."[96] By broadening his definition of "organic units," Darwin could still argue that sub-cellular gemmules could produce cells, despite the increasing strength of Virchow's position.

Darwin's allegiance to older cellular theories indicates that he had been developing various hypotheses concerning inheritance, variation, and development, or "generation," since the late 1830's and early 1840's. In a letter to Lyell dated August 22, 1867, he stated, "I do not know whether you ever had the feeling of having thought so much over a subject that you had lost all power of judging it. This is my case with Pangenesis (which is 26 or 27 years old), but I am inclined to think that if it be admitted as a probable hypothesis it will be a somewhat important step in Biology."[97] The assumptions out of which he built his particular theory of variation and heredity originated in the cellular theories of the 1830s and 1840s.[98] Thus, the non-committal diplomatic stance Darwin adopted in the passage above (n. 96), was probably

[93] Barrett, 1980, II, pp. 158–160.

[94] Ibid., p. 159.

[95] See Hodge, 1985, pp. 236–237.

[96] Darwin, *Variation* (1868), II, p. 444. Darwin, *Variation* (1875), II, p. 366 contains a similar passage.

[97] Darwin, F., 1959, II, p. 255.

[98] See Hodge, 1985, pp. 231–237; Robinson, 1979, p. 5. For a somewhat opposing view, see Geison, 1969, p. 380.

an outcome of the tension between his commitments and the increasingly powerful newer cellular theory.

For Darwin, the study of heredity required the study of development because the latter study would delineate when, where, in what quantity, in what types, and by which mechanisms the hereditary particles, the gemmules, would be produced. A study of development would show how gemmules interacted with other pre-existing cells, other gemmules and external conditions of life to produce more cells, tissues and organs. Such a study would also indicate how these cells, tissues and organs interacted with external conditions to produce more gemmules. If, for some set of characters, the developmental path (from gemmule to character) of the offspring was similar to the path of the parent, inheritance had occurred; if the developmental path was different from the path of the parent, variation had occurred.

With Pangenesis, Darwin could now suggest possible physiological mechanisms underlying germinally-mediated and somatically-mediated variations. Concerning the first type of variation he asserted: "Variability often depends, as I have attempted to show, on the reproductive organs being injuriously affected by changed conditions; and in this case the gemmules derived from the various parts of the body are probably aggregated in an irregular manner, some superfluous and others deficient."[99] Concerning the second type of variation he stated: "In variations caused by the direct action of changed conditions, whether of a definite or indefinite nature, as with the fleeces of sheep in hot countries, with maize grown in cold countries, with inherited gout, &c., the tissues of the body, according to the doctrine of pangenesis, are directly affected by the new conditions, and consequently throw off modified gemmules, which are transmitted with their newly acquired peculiarities to the offspring."[100] Darwin had now postulated mechanisms for how the environment caused variation in both the reproductive organs and the body.[101] In the former case, the environment caused the reproductive organs to aggregate gemmules in disorderly ways; such variation was displayed only in the offspring. In the latter case, the environment induced organs to change and produce altered gemmules; such variation was displayed in the parent as well as the offspring.

In Figure 1 we see that when changes in the conditions of life caused somatically-mediated variation, the body was affected (1) and emitted modi-

[99] Darwin, *Variation* (1868), II, p. 471 and Darwin, *Variation* (1875), II, p. 388. The two editions contain the same passage.

[100] Darwin, *Variation* (1868), II, p. 472. Darwin, *Variation* (1875), II, p. 388 contains a similar, but shorter passage, where the examples and the reference to Pangenesis are omitted.

[101] See also Darwin, *Variation* (1868), II, p. 474 and Darwin, *Variation* (1875), II, p. 390.

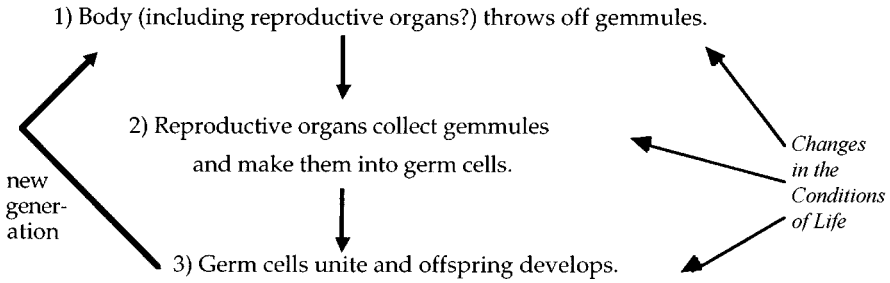

Figure 1. A representation of a life-cycle during which variation and heredity occur, according to Darwin.

fied gemmules. When changes in the conditions of life caused germinally-mediated variation, the reproductive organs were affected (2) and collected gemmules irregularly. Changes in the conditions of life could also alter the development of the offspring (3), which led either to reversion or to another change in the reproductive organs or body. These variations might, in turn, be inherited by the offspring of that offspring.

Darwin saw the reproductive organs as part of the "organisation" (the body).[102] But he singled them out as a *special locus* for environmental action. Darwin, however, was not explicit about whether or not the reproductive organs themselves emitted gemmules. It only seems logical that they must do so because that would be the only way the reproductive organs could be reproduced. Darwin did not state whether the environment could act "indirectly" as well as "directly" on the reproductive organs. For example, could the environment cause an ovary to grow larger causing it to collect gemmules in an irregular manner as well as to emit modified gemmules that were then collected by the same ovary? Darwin elided this question. In granting the reproductive organs special status, he assumed that their main function was to collect and reproduce gemmules from the rest of the body, but not to produce their own gemmules.

Darwin had now suggested a material and mechanical explanation for both variation and heredity. No longer did he allude to abstract "powers," as in the *Essay of 1844*, nor did he provide vague generalizations, as in *On the Origin of Species* (1859). Pangenesis tied variation, heredity, and development together into a coherent developmental theory of heredity.

[102] See Peckham, 1959, pp. 80, 276.

Transmission vs. Development

The distinction between the transmission and the development of organic units became important just after the turn of the twentieth century.[103] It may seem surprising that Darwin also made this distinction. He wrote: "Two distinct elements are included under the term 'inheritance,' namely the transmission and development of characters; but as these generally go together, the distinction is often overlooked."[104] Darwin was not using the distinction in the modern sense, however. When making it, he always referred to his hypothesis of Pangenesis.[105] The importance of context in determining meanings of scientific terms is apparent in the way that Darwin used this distinction.[106]

Analyzing one passage will allow us to see how such meanings depend on context. Darwin asked: "What can be more wonderful than that some trifling peculiarity, not primordially attached to the species, should be *transmitted* through the male or female sexual cells, which are so minute as not to be visible to the naked eye, and afterwards through the incessant changes of a long course of *development*, undergone either in the womb or in the egg, and ultimately appear in the offspring when mature, or even when quite old, as in the case of certain diseases?"[107] In this passage, transmission referred to one specific stage of the life-cycle. Transmission occurred "through the . . . sexual cells." The material gemmules that transmitted this character did not necessarily express it in the next (offspring) generation; gemmule development depended on environmental circumstances and the presence of other gemmules. If these gemmules did direct the development of the relevant body part, it would then produce more of them. But they still might not be subsequently transmitted to the next (grand-offspring) generation. Gemmules could be lost, although Darwin provided no mechanism for this.[108] In short, the process of transmission was contingent on the development of the organism. Furthermore, transmission was not sequestered from environmental influences in Darwin's theory, nor did a certain lineage of cells

[103] Allen, 1985; Churchill, 1980; Gerson, 1998; Maienschein, 1987.

[104] Darwin, *Descent* (1871), I, p. 279.

[105] Ibid., I, p. 280. See below, n. 107 for two other passages with the distinction.

[106] Kuhn (1970) made this point concerning the meanings of terms like mass and space in the Newtonian and Einsteinian frameworks. He wrote: "This need to change the meaning of established and familiar concepts is central to the revolutionary impact of Einstein's theory" (Kuhn, 1970, p. 102).

[107] Darwin, *Variation* (1868), II, p. 10 and Darwin, *Variation* (1875), I, p. 446 (emphasis mine). The two editions contain the same passage. For another passage which makes the distinction, see Darwin's response to Delpino. Barrett, 1980, II, p. 160.

[108] See Darwin, *Variation* (1868), II, p. 480 and Darwin, *Variation* (1875), II, p. 396.

exist continuously. Both these meanings of transmission are distinct from modern meanings.

Other historians also share the view that Pangenesis, Darwin's explicitly formulated theory of heredity, was primarily a developmental theory that included transmission. Concerning Pangenesis, Michael Ghiselin writes, "[Pangenesis] had to do with what we now call genetics, but, like our contemporary molecular genetics, its primary concern was with *developmental*, rather than with *transmissional*, genetics."[109] With respect to the putative distinction between large and small (discontinuous vs. continuous) variation, Ghiselin writes: "He [Darwin] saw no qualitative difference between the two kinds of variation – large or small, they could all be interpreted as modifications of developmental mechanisms."[110] In a similar vein, Bowler writes: "It was almost impossible[111] for a nineteenth-century biologist [like Darwin] to conceive of a study that would concentrate solely on the transmission of characters, bypassing the problem of how those characters were developed in the growing organism."[112] After the turn of the twentieth century, development was understood as a product of transmission. But for Darwin transmission was a product of development.

Conceptualizing Heredity and Variation: Opposition or the Inheritance of Variation?

Now that we have covered Darwin's views concerning development and variation, we will turn our attention to the relationship he saw between heredity and variation. On the one hand, Darwin perceived a tension between the two.[113] On the other hand, he also stressed the importance of the inheritance *of* variation.

Concerning the tension, Darwin wrote in *On the Origin of Species*, "inheritance of every character whatever [is] the rule, and non-inheritance [is] the anomaly."[114] Thus, inheritance was more common than non-inheritance, and they were conceptualized as two distinct categories. In *The Variation of Animals and Plants*, Darwin stated that "[a] large number of cases of non-inheritance are intelligible on the principle, that a strong tendency to inheritance does exist, but that it is overborne by hostile or unfavourable conditions

109 Ghiselin, 1975, p. 47.

110 Ghiselin, 1973, p. 158.

111 Gregor Mendel would have been an exception; presumably he accounts for why Bowler writes "almost impossible."

112 Bowler, 1990, p. 211.

113 See Churchill, 1987, pp. 343–346.

114 Peckham, 1959, p. 86. Darwin kept this phrase intact throughout all six editions.

of life."[115] He also asserted that "[m]any cases of non-inheritance apparently result from the conditions of life continually inducing fresh variability."[116] Thus, an opposition existed between inheritance and externally-induced variation, the latter being a sub-set of cases of non-inheritance. But Darwin was not alluding to two separate "laws", one for inheritance and one for variation, as his influential contemporary Prosper Lucas did.[117] A dictum, similar to Newton's first law, might summarize Darwin's commitments regarding inheritance and variation: *constant characters as well as variations, once they occur, breed true unless enacted upon by changes in the environment.*

This dictum does not fully describe Darwin's views since Pangenesis postulated a deep relation between variation and heredity. He did not give primary importance to one at the expense of the other, nor did he always associate variation with the existence of "non-inheritance." With Pangenesis, as we have seen, he provided a material and mechanistic explanation of how the environment induced variation and how this variation was inherited.

Darwin was also aware that his theory required the inheritance *of* variation. He asserted that "[a]ny variation which is not inherited is unimportant for us."[118] He realized that the inheritance of variation was necessary for evolution to occur and assumed that every variation was potentially heritable in the subsequent generation. As we saw above, Darwin held inheritance to be more common than non-inheritance. Presumably he also meant that the inheritance of variation (parents differ from grandparents; offspring are similar to parents) was more common than the non-inheritance of variation. Although cases of the inheritance of variation would seem to be special cases of inheritance, Darwin was unclear about this.

By examining an example of heredity in the chapter on Pangenesis, we will observe his concern both with the inheritance of variation and with heredity as a developmental process. Darwin wrote: "If we suppose a homogenous gelatinous protozoon to *vary* and assume a reddish colour, a minute *separated* atom would *naturally*, as it *grew* to full size, *retain* the same colour; and we should have the simplest *form of inheritance*."[119]

[115] Darwin, *Variation* (1868), II, p. 37 and Darwin, *Variation* (1875), I, p. 470. The two editions contain the same passage.

[116] Darwin, *Variation* (1868), II, p. 38 and Darwin, *Variation* (1875), I, p. 471. The two editions contain the same passage.

[117] Churchill, 1987, pp. 342–343.

[118] Peckham, 1959, p. 85. Darwin kept this sentence intact throughout all six editions.

[119] Darwin, *Variation* (1868), II, pp. 474–475 (emphasis mine). See also Darwin, *Variation* (1875), II, pp. 390–391. The only difference between the passages in the two editions is that "atom" is replaced by "particle" in the 1875 edition. As we saw in the passage of n. 96 above, Darwin was making his Pangenesis theory less committed to any particular cytological theory, so perhaps he was searching for a more neutral term. In both editions Darwin also provided

He then continued: "Precisely the same view may be extended to the infinitely numerous and diversified units of which the whole body in one of the higher animals is composed; and the separated atoms are our gemmules."[120] Thus, the inheritance of variation, and heredity as a developmental process, held for higher animals as well. But Darwin did not resolve the myriad subtle tensions between variation – the production and existence of inter-generational differences, and heredity – the production and existence of inter-generational similarities. He held contrary claims. Sometimes he saw the two in opposition, sometimes as part of one developmental process.

Combining Darwin's externalist position on the causes of variation with his developmental theory of heredity, and using the idea of the inheritance of variation, we could rewrite the above dictum as: *life-cycles produce life-cycles similar to themselves unless enacted upon by changes in the environment, in which case they often produce life-cycles different from themselves which, in turn, produce life-cycles similar to themselves unless enacted upon by changes in the environment*. This dictum emphasizes that it is life-cycles that are being generated; it is recursive to emphasize the continual production of new generations of life-cycles. The dictum summarizes Darwin's externalist views on the causes of variation and his developmental theory of heredity. For him, inheritance and the inheritance of variation occurred in unchanging environments, and, in some cases, in changing environments (see above, n. 47); variation necessarily happened in changing environments.

In summary, Darwin was committed to a developmental theory of heredity. This commitment, stemming from early in his career, was elaborated in his hypothesis of Pangenesis. Pangenesis provided materialistic mechanisms for germinally-mediated and somatically-mediated variations. Furthermore, within the context of this hypothesis, Darwin distinguished between transmission and development. These terms have meanings distinct from twentieth-century ones. Pangenesis provided a way for Darwin to integrate his commitments to external causes of variation, heredity as a developmental process, and the inheritance of variation.

a footnote to a passage from Haeckel's *Generelle Morphologie*, "Lediglich die partielle Identität der specifisch-constituirten Materie im elterlichen und im kindlichen Organismus, die Theilung dieser Materie bei der Fortpflanzung, ist die Ursache der Erblichkeit" (Haeckel, 1866, II, p. 171). In English: "Merely the partial identity of the specifically constituted material in the parental and the offspring organism, [that is] the splitting of this material in the act of procreation, is the cause of heredity" (trans. Peter Gilgen and Frederick Churchill). Although Darwin's views differed from Haeckel's in a number of ways, both biologists held developmental theories of heredity. See Robinson (1979) for a description of Haeckel's views.

[120] Darwin, *Variation* (1868), II, p. 475. Darwin, *Variation* (1875), II, p. 391 contains a similar passage. The important difference is that "atoms" was again replaced by "particles" (see above, n. 119).

Toward a Complete Understanding of Darwin's Theory of Variation and Heredity

Darwin's views on variation, heredity, and development differ markedly from modern positions. First, he held that environmental changes, acting either on the reproductive organs or the body, were necessary to produce variation. Second, heredity was a developmental, not a transmissional, process. Germinally-mediated and somatically-mediated variations, which were necessarily caused by the environment, were a change in the development of the organism and/or its offspring. A change in developmental pattern was a variation; constancy in developmental pattern constituted inheritance.

While Darwin adopted externalist and developmental positions already in his notebooks, he elaborated an explicit theory of variation, heredity, and development only with Pangenesis. The relations between changing environments, organism, and the gemmules it contained determined both variation and heredity. Pangenesis was developmental not only because the whole life-cycle was analyzed, but also because it showed how gemmules that developed in the existing generation, and gemmules that were transmitted to the next one, depended causally on multiple factors, including environmental and somatic influences. Many of the views embodied in Pangenesis had their seeds in Darwin's research and thought during the late 1830s and early 1840s.

Among nineteenth-century biologists, Darwin was not alone in his externalist and developmental points of view. In fact, August Weismann, famous for disproving some of the notions Darwin took for granted, held versions of these two beliefs in common with Darwin.[121] A complete comparative story of late nineteenth-century views on variation remains to be told.

Acknowledgments

I am grateful to the following for comments and support: Mark Brown, Frederick Churchill, Richard Francis, Elihu Gerson, Michael Ghiselin, Peter Gilgen, Peter Godfrey-Smith, James Griesemer, John den Hartog, Peter Kessler, Sandhya Kilaru, Timothy Lenoir, Jane Maienschein, Linda Mishkin, Amir Najmi, Susan Oyama, Aage and Grethe Winther, my sister, Rikke Winther, and three anonymous reviewers.

[121] Winther, in prep.

References

Allen, Garland E. 1985. “Heredity under an Embryological Paradigm: The Case of Genetics and Embryology.” *The Biological Bulletin* 168: 107–121.

Barrett, Paul (ed.). 1980. *The Collected Papers of Charles Darwin*, 2 vols. Chicago: University of Chicago Press.

Barrett, Paul, Peter J. Gautrey, Sandra Herbert, David Kohn and Sydney Smith (eds.). 1987. *Charles Darwin’s Notebooks, 1836–1844*. British Museum (Natural History) and Ithaca: Cornell University Press.

Bowler, Peter J. 1974. “Darwin’s Concepts of Variation.” *Journal of the History of Medicine and Allied Sciences* 29: 196–212.

—— 1984. *Evolution: The History of an Idea*. Berkeley: University of California Press.

—— 1990. *Charles Darwin: The Man and His Influence*. Cambridge, UK: Cambridge University Press.

Burchfield, Joe D. 1990. *Lord Kelvin and the Age of the Earth*. Chicago: University of Chicago Press.

Burkhardt, Frederick, Duncan M. Porter, Joy Harvey and Jonathan R. Topham (eds.). 1997. *The Correspondence of Charles Darwin*, Vol. 10, p. 1862. Cambridge, UK: Cambridge University Press.

Churchill, Frederick B. 1980. “The Modern Evolutionary Synthesis and the Biogenetic Law.” In *The Evolutionary Synthesis: Perspectives on the Unification of Biology*, ed. Ernst Mayr and William B. Provine, pp. 112–122. Cambridge, MA: Harvard University Press.

—— 1987. “From Heredity Theory to *Vererbung*. The Transmission Problem, 1850–1915.” *Isis* 78: 337–364.

Darwin, Charles R. 1868. *The Variation of Animals and Plants Under Domestication*, 1st edn., 2 vols. New York: Orange Judd & Co.

—— 1896. *The Variation of Animals and Plants Under Domestication (1875)*, 2nd edn., 2 vols. New York: D. Appleton Company.

—— 1958. *Sketch of 1842*. In *Evolution by Natural Selection*, commentary by Gavin De Beer, pp. 41–88. Cambridge, UK: Cambridge University Press.

—— 1958. *Essay of 1844*. In *Evolution by Natural Selection*, commentary by Gavin De Beer, pp. 91–254. Cambridge, UK: Cambridge University Press.

—— 1981. *The Descent of Man, and Selection in Relation to Sex*, 1st edn., 2 vols. Princeton: Princeton University Press.

—— 1984. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life (1859)*, 1st edn. Cambridge, MA: Harvard University Press.

Darwin, Francis. 1903. *More Letters of Charles Darwin*, 2 vols. London: John Murray.

—— 1959. *The Life and Letters of Charles Darwin*, 2 vols. New York: Basic Books.

Desmond, Adrian and James R. Moore. 1991. *Darwin: The Life of a Tormented Evolutionist*. New York: Warner Books.

Geison, Gerald L. 1969. “Darwin and Heredity: The Evolution of His Hypothesis of Pangenesis.” *Journal of the History of Medicine and Allied Sciences* 24: 375–411.

Gerson, Elihu M. 1998. “The American System of Research: Evolutionary Biology, 1890–1950.” Sociology Dissertation, University of Chicago.

Ghiselin, Michael T. 1969. *The Triumph of the Darwinian Method*. Berkeley: University of California Press.

—— 1973. “Mr. Darwin’s Critics, Old and New.” *Journal of the History of Biology* 6: 155–165.

—— 1975. “The Rationale of Pangenesis.” *Genetics* 79: 47–57.

Godfrey-Smith, Peter. 1996. *Complexity and the Function of Mind in Nature*. Cambridge, UK: Cambridge University Press.

Gould, Stephen J. 1977. "Eternal Metaphors of Palaentology." In *Patterns of Evolution as Illustrated by the Fossil Record*, ed. Anthony Hallam, pp. 1–26. Amsterdam: Elsevier.

Griesemer, James R. 1993. "The Informational Gene and the Substantial Body: On the Generalization of Evolutionary Theory by Abstraction." Department of Philosophy, University of California, Davis.

—— In prep. *Reproduction in the Evolutionary Process*.

Haeckel, Ernst. 1866. *Generelle Morphologie*, 2 vols. Berlin: Reimer.

Hodge, M. J. S. 1985. "Darwin as a Lifelong Generation Theorist." In *The Darwinian Heritage*, ed. David Kohn, pp. 207–243. Princeton: Princeton University Press.

Hull, David L. 1973. *Darwin and His Critics*. Chicago: University of Chicago Press.

Kohn, David. 1980. "Theories to Work By: Rejected Theories, Reproduction, and Darwin's Path to Natural Selection." In *Studies in the History of Biology*, ed. William Coleman and Camille Limoges, vol. 4, pp. 67–170. Baltimore: Johns Hopkins University Press.

Kuhn, Thomas S. 1970. *The Structure of Scientific Revolutions*, 2nd edn. Chicago: University of Chicago Press.

Levins, Richard and Richard C. Lewontin. 1985. *The Dialectical Biologist*. Cambridge, MA: Harvard University Press.

Maienschein, Jane. 1987. "Heredity/Development in the United States, circa 1900." *History and Philosophy of the Life Sciences* 9: 79–93.

Olby, Robert C. 1963. "Charles Darwin's Manuscript of *Pangenesis*." *British Journal for the History of Science* 1: 250–63.

—— 1966. *Origins of Mendelism*. New York: Schocken Books.

Ospovat, Dov. 1981. *The Development of Darwin's Theory: Natural History, Natural Theology, and Natural Selection, 1838–1859*. Cambridge, UK: Cambridge University Press.

Oyama, Susan. 1985. *The Ontogeny of Information: Developmental Systems and Evolution*. Cambridge, UK: Cambridge University Press.

Peckham, Morse (ed.). 1959. *The Origin of Species by Charles Darwin: A Variorum Text*. Philadelphia: University of Pennsylvania Press.

Richards, Robert J. 1992. *The Meaning of Evolution*. Chicago: University of Chicago Press.

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

Vorzimmer, Peter. 1963. "Charles Darwin and Blending Inheritance." *Isis* 54: 371–90.

—— 1970. *Charles Darwin: The Years of Controversy. The Origin of Species and Its Critics 1859–1882*. Philadelphia: Temple University Press.

Weismann, August. 1868. *Über die Berechtigung der Darwin'schen Theorie*. Leipzig: Wilhelm Engelmann.

—— 1875. "Über den Saison-Dimorphismus der Schmetterlinge." In *Studien zur Descendenz-Theorie*, 2 vols., pp. 1–94. Leipzig: Wilhelm Engelmann.

—— 1882. "On the Seasonal Dimorphism of Butterflies." In *Studies in the Theory of Descent*, translated by Raphael Meldola, pp. 1–160. London: Sampson Low, Marston, Searle, & Rivington.

Winther, Rasmus. In prep. "Weismann on Germ-Plasm Variation." Presented at the 1999 Meetings of the International Society for the History, Philosophy, and Social Studies of Biology in Oaxaca, Mexico, July 7–11, 1999.

Zirkle, Conway. 1946. "The Early History of the Idea of the Inheritance of Acquired Characters and of Pangenesis." *Transactions of the American Philosophical Society* 35: 91–151.