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Lamarck Ascending!

A Review of *Transformations of Lamarckism: From Subtle Fluids to Molecular Biology*. Edited by Snait B. Gissis and Eva Jablonka, MIT Press, 2011

David Haig[§]

Transformations of Lamarckism is an edited volume arising from a workshop to commemorate the bicentenary of the publication of *Philosophie Zoologique*. The contributed chapters discuss the history of Lamarckism, present new developments in biology that could be considered to vindicate Lamarck, and argue for a revision, if not a revolution, in evolutionary theory. My review argues that twentieth and twenty-first century conceptions of Lamarckism can be considered a reaction to August Weismann's uncompromising rejection of the inheritance of acquired characters in the late nineteenth century. Weismann rejected the inheritance of acquired characters both as a proximate mechanism of heredity and as an ultimate cause of adaptation. I argue that Weismann's proximate claim is still valid for the kind of mechanism that he had in mind but that the inheritance of acquired characters has come to refer to many different processes, some of which undoubtedly do occur. However, processes of physiological adaptation and adaptive plasticity, even if transgenerational, do not challenge Weismann's claim about the ultimate causes of adaptation because these processes can be understood as evolving by natural selection. Finally, I discuss some of the emotional and aesthetic reasons why many find Lamarckism an attractive alternative to hard-core neo-Darwinism.

KEYWORDS

Epigenetic inheritance • Inheritance of acquired characters • Lamarck • Natural selection • Niche construction • Phenotypic plasticity • Proximate/ultimate • Weismann

2009 was a banner year for anniversaries: the 250th anniversary of the *Theory of Moral Sentiments*, the 200th anniversary of Charles Darwin's birth, and the 150th anniversary of *On the Origin of Species*. Almost lost in the flurry of celebratory symposia was the 200th anniversary of Lamarck's *Philosophie Zoologique*. Almost, but not quite, forgotten. Snait Gissis and Eva Jablonka organized a commemorative workshop in Jerusalem with two aims: "first, to redress a critical lapse in historical memory … and, second, to bring into focus new developments in biology that make Lamarck's ideas relevant not only to modern empirical and theoretical research, but also to problems in the philosophy of biology and to the writing of the history and sociology of evolutionary theory" (xi). *Transformations of Lamarckism* (*ToL*) is the product of that workshop. It contains 41 short chapters (#1–#41) written by a distinguished group of historians, biologists, and philosophers.

The historiography of evolutionary biology is replete with tales of heroes triumphing over adversaries. Jean-Baptiste Antoine de Monet, Chevalier de la Marck, has served repeatedly in both roles. The process

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began long before the *Origin of Species*, with the reactionary Georges Cuvier cast as adversary to the heroic Lamarck. "The myth of the poor, isolated, and blind Lamarck was created and diffused by his supporters at the height of his success with the reading public and the intellectual elites" (Corsi #2, 15). Since the *Origin*, "Lamarck has served alternately as a foil and an ally to Darwin. Darwin's supporters have tried in various ways either to appropriate Lamarck as a precursor and partner, or else to define Lamarckism narrowly and to dismiss it as naive and obsolete. Contrarily, Darwin's rivals have tried to redefine Lamarck as a figurehead for their own theories and approaches" (Gliboff #5, 45–46). As both Corsi and Gliboff remark, the narrative uses of Lamarckism often have a tenuous relation, at best, to what Lamarck actually wrote or taught.

One of the strengths of *ToL* is the historical survey it provides of Lamarckian ideas and their impact. Gliboff (#5) identifies the period from Haeckel's *Generelle Morphologie* in 1866 to Kammerer's suicide in 1926 as the Golden Age of Lamarckism. A diversity of neo-Lamarckian positions were held during this period, with distinctive Lamarckian traditions in Germany (Gliboff #5), France (Loison #7) and the Soviet Union (Roll-Hansen #8). Charlotte Weissman (#6) describes how August Weismann developed the concept of germinal selection to cope with Lamarckian challenges to his theories. His was an early levels-of-selection argument in which nonadaptive trends were explained by competition among elements within the germ-plasm (germinal selection) that proceeded more-or-less independently of competition among individual organisms (personal selection). Gissis (#9) discusses the role of Lamarckian ideas in the sociological thought of Herbert Spencer and Émile Durkheim. Subsequent chapters (#10–#14) discuss the marginalization of 'soft inheritance' during the Modern Synthesis of the 1930s and 1940s.

In her introduction to a series of chapters (#15–#27) on Lamarckian problematics in biology, Jablonka argues that the comfortable orthodoxies of the Modern Synthesis have been recently challenged by a revival of interest in Lamarckian ideas, spurred by renewed attention to developmental mechanisms, phenotypic plasticity, and mechanisms of epigenetic inheritance. Many, although not all, of the authors of these chapters appear to share Jablonka's view that there is something rotten in the Modern Synthesis. This section contains much interesting biology but I will not review it in detail; rather, I will address the question of whether any of these phenomena require a revolution, as distinct from evolution, in evolutionary theory.

Appeals to Lamarckian inheritance never entirely disappeared in the years since the Modern Synthesis. Every few years, the popular press announces that some scientist has vindicated Lamarck by showing that an acquired character is inherited. After a short period of attention, each of these claims has, for the most part, been forgotten. One can interpret this either as a measure of the soundness of standard theory or the resistance to change of an established orthodoxy. But the repeated pattern suggests elements of the scientific community, and of the general public, feel uncomfortable with the preeminent role assigned to natural selection in evolutionary theory. In recent years, epigenetics has been repeatedly characterized as allowing a distinctly Lamarckian form of inheritance and such claims have attained wide currency.

Griesemer (#31, 331) observes, correctly I believe, that most of the claims that epigenetic inheritance requires a significant, perhaps revolutionary, reformulation of evolutionary theory "come from mechanistic molecular (MM) biology rather than from quantitative evolutionary (QE) specialties." He proposes that this contrast arises from the different outlooks of these two major branches of biology. The changes required appear modest from the perspective of MM science but would be revolutionary from the perspective of QE theory ("a paradigm shift"). This diagnosis seems a little odd. MM scientists, for whom the change is straightforward, trumpet the conceptual shift as revolutionary, whereas QE scientists, for whom the change would be radical, dismiss it as 'nothing special.'

I would reverse the diagnosis. Epigenetic inheritance is perceived as radical by some MM biologists because it overturns some of their basic mechanistic assumptions, such as the Central Dogma of molecular biology, whereas the theoretical changes required for QE theory are rather modest because QE models are largely independent of molecular mechanisms. After all, the basic models of evolutionary population genetics were developed before it was known that genes 'are DNA' and these models should be unaffected by whether a 'mutation' is caused by a change in nucleotide sequence or a change in cytosine methylation (Haig 2007). A justification of my alternative diagnosis will require a digression on the kinds of 'Lamarckian' observations that are easily accommodated within current paradigms and the kinds that would require a radical change to existing theory.

A belief that traits acquired during an individual's life are passed on to offspring was commonplace both before and after Lamarck. His novel contribution was to assert that the cumulative effects of use and disuse could effect major morphological changes and bring new species into existence (Burkhardt #4). The quintessential Lamarckian phrase 'inheritance of acquired characters' is not found in books in the English language prior to the mid-1880s but then rises rapidly to levels that are maintained for 50 years until a decline in the 1930s with the Modern Synthesis (Google Books Ngram Viewer). 'Lamarckian' shows a similar rapid rise in the mid-1880s. This timing suggests that the genesis of modern rhetorical uses of Lamarck can be traced to disputes between supporters and opponents of Weismann in the 1880s and 1890s.

Weismann and his followers rejected the inheritance of acquired characters and promoted the all-sufficiency of natural selection. Their strident language provoked a strong response from Darwinian pluralists and from others skeptical of the explanatory power of natural selection. Romanes (1888) wrote "The consequence of this kind of writing is that anyone who, like myself, still retains unmodified the Darwinism of Darwin himself, is ticketed as a follower of Lamarck … The school of Weismann may properly be called Neo-Darwinian: pure Darwinian it certainly is not." And thus, neo-Darwinism entered the English language. Moreover, the polarizing message of the neo-Darwinists appears to have induced some scientists, who might not otherwise have done so, to identify themselves as latter-day Lamarckists. From a historical perspective, neo-Darwinism can be considered to have lost the argument because, in the ensuing decades, most biologists assigned a relatively modest or negligible role to natural selection in evolutionary change (Bowler 1983).

For Weismann, Lamarckism failed both as a proximate explanation of heredity and as an ultimate explanation of adaptation (to use modern parlance). There is a logical asymmetry between the two parts of his argument. If the proximate claim is accepted, then the inheritance of acquired characters can be neither a mechanism of heredity nor a source of adaptation. However, if the proximate claim is rejected, then the ultimate claim, that natural selection is the only source of adaptation, could still be valid. Weismann's rejection of the inheritance of acquired characters as a mechanism of heredity is clearer than his rejection of it as a source of adaptation, perhaps because he recognized that the logical primacy of the proximate claim rendered a detailed argument for the second claim superfluous.

Weismann's dismissal of Lamarckism as a proximate mechanism of heredity is straightforward. He conceded that the environment could influence the germ-plasm, via the soma, but rejected the notion that a change in the soma could cause a correlated change in the germ-plasm that would cause the modified character to be faithfully inherited by offspring. He based this rejection on the assumption that character and determinants were different kinds of things, with different molecular structures, not on the spatial separation of soma and germ-plasm (Haig 2007). In his view, the inheritance of acquired characters presupposes some form of preformation of characters in the germ-plasm and is rendered unintelligible by the epigenetic nature of development (Weismann 1891, 324–327). As a pleasing irony, modern critics of Weismann often invoke an emphasis on epigenesis and developmental mechanisms as part of the appeal of a Lamarckian perspective.

Weismann (1893) rejected the inheritance of acquired characters as a cause of adaptation because natural selection was not only an all-sufficient explanation of adaptation, but the only conceivable naturalistic explanation. He wrote, "we must assume natural selection to be the principle of explanation of the metamorphoses, because all other apparent principles of explanation fail us, and it is inconceivable that there could yet be another capable of explaining the adaptations of organisms, *without assuming the help of a principle of design*. In other words, *it is the only conceivable natural explanation of organisms regarded as adaptations to conditions*" (328; emphases in original).

Arguments that only one explanation is conceivable are dubious because of the implied claim of omnipotence, but I have never seen a convincing argument for how the inheritance of acquired characters, by itself, can give rise to evolutionary adaptation without either an appeal to pre-existing design or to natural selection at some stage in the process (Haig 2007). There is nothing intrinsic to the inheritance of the effects of use and disuse that ensures a better fit to the environment. Why shouldn't repeated use of an organ cause it to become more and more feeble in each generation rather than stronger and stronger? In *Philosophie Zoologique*, the necessary directionality was provided by Lamarck's 'First Law' that described the properties of the 'power of life.' Lamarck saw this as a necessary complement to his 'Second Law' that described the

inheritance of acquired changes (Burkhardt #4; Loison #7). Weismann undoubtedly considered the First Law to be a surreptitious importation of an inadmissible 'principle of design.'

A violation of either of Weismann's conclusions, about the proximate mechanism of inheritance or about the ultimate source of adaptation, would require a radical change in current evolutionary theory. But it is important to be clear about the specific nature of his conclusions. With respect to the mechanism of heredity, Weismann rejected, on principle, a mode of inheritance in which a change in the soma directly caused changes in the germ-plasm that recapitulated the somatic change in subsequent generations. Unfortunately, the 'inheritance of acquired characters' has come to mean many different things to different people and Weismann's arguments do not apply to all possible interpretations of the phrase. For this reason, I have advocated abandoning the phrase, as close to meaningless, and specifying in each particular case what is being inherited (effects of use and disuse, mutilations, methylation patterns, symbionts, plasmids) and how the 'character' was 'acquired.' When this is done, most theoretical disagreements evaporate (Haig 2007). With respect to the ultimate source of adaptation, current evolutionary theory would be challenged by mechanisms of physiological adaptation and adaptive plasticity (within or between generations), but only if these proximate mechanisms could be shown to have evolved by processes other than natural selection.

None of the contributors to *ToL* defend the kind of hereditary mechanism rejected by Weismann but some expand Lamarckian inheritance to include all forms of 'soft inheritance.' Gissis and Jablonka (#10, 105) adopt Mayr's definition of soft inheritance as "a gradual change of the genetic material itself, either by use or disuse, or by some internal progressive tendencies, or through the direct effect of the environment," although it is clear that they do not limit the concept to 'gradual' changes. Soft inheritance is an elastic concept but includes mechanisms of cellular epigenetic inheritance such as DNA methylation, self-sustaining regulatory loops, structural templating, and RNA interference (Jablonka #21). In a review of Jablonka and Lamb's *Evolution in Four Dimensions* (2005), I have argued that such mechanisms are 'tools' (proximate devices) that can be exploited by natural selection to enable organisms, or their genes, to respond adaptively to different environments (Haig 2007; see also Scott-Phillips et al. 2011). It seems a matter of personal preference whether these mechanisms are seen as Lamarckian. It is likewise a matter of personal preference whether these mechanisms are seen as enriching or challenging neo-Darwinism.

Newman and Bhat (#16, 166) write, "Phenotypic plasticity and niche construction are two phenomena that can individually be accommodated by the Modern Synthesis. But taken together they obviate the need for gradualist and adaptationist scenarios. Large-scale (i.e., saltational) phenotypic changes can occur in the space of a single lifetime due to the dynamics of development, and the forms that result, not being passive candidates for places in preexisting niches, will invent unique ways of life." I agree with the first sentence but disagree with the second. I also agree with the first part of the third sentence, but do not have allotted space to undertake a textual deconstruction of the second part.

Phenotypic plasticity is "broadly defined as the ability of a single genotype to express different phenotypes in different environments" (Sultan #19, 193). Such phenomena have long been studied by ecologically-minded neo-Darwinists. If the ability to make a plastic response is possessed by all members of a population, such that all phenotypic differences are due to exposure to different environmental triggers, in this generation or preceding generations, then there is no heritable variation for current natural selection. This does not mean that adaptive plasticity has not evolved by past natural selection. If individuals vary in their repertoires of plastic responses to environmental triggers, then these repertoires are subject to natural selection. Neo-Darwinists prefer to emphasize how adaptive plastic responses have arisen by natural selection on an evolutionary timescale whereas neo-Lamarckists prefer to emphasize how phenotypic plasticity allows organisms to adapt to fluctuating environments on an ecological timescale, but there is no irreconcilable conflict between these perspectives.

Niche construction "refers to a process by which organisms, through their metabolism, physiology, behavior, and dispersal, causally affect abiotic and biotic features of their environment. By doing so organisms generate feedback from their environment that may operate on both ecological and evolutionary timescales" (Shavit and Griesemer #29, 307). Such phenomena are well known to ecologically-minded neo-Darwinists. Organisms have abilities to select the environments they experience and to modify these environments, whether these are Darwin's earthworms transforming the soil within which they live, seeds

that germinate after fire, branches that grow toward light, or, on a grander scale, cyanobacteria that poisoned the atmosphere for anaerobic life.

A comment by Shavit and Griesemer (#29, 308) is revealing: "For classical neo-Darwinists to admit niche construction and incorporate it into their practices, a detailed mathematical model of this process is required which represents organisms as causes of environmental states and dependence of selection pressures feeding back to organisms on those same environmental parameters." Shavit and Griesemer seem to equate classical neo-Darwinism with theoretical population genetics, although this is not the only strand within the Modern Synthesis. It would certainly not describe Ernst Mayr and his disdain for 'beanbag genetics' nor would the construction of 'detailed mathematical models' describe the work of Richard Dawkins. Even among mathematically-inclined neo-Darwinists, there have been deep divisions on how to model the evolutionary process, although these differences often resolve into a preference for different kinds of questions on different time-scales (Eshel 1996). Some strands of neo-Darwinism have no problem with niche construction although they might choose to call it by a different name.

It seems to me that arguments between supporters and critics of the Modern Synthesis often are based on differences of preference and thinking style rather than matters of substance. Modern neo-Lamarckists and neo-Darwinists both encompass a range of outlooks, but the neo-Lamarckians, considered in aggregate, have a distinctive set of preferences, including: a preference for proximate over ultimate explanations; a preference for development over selection; a preference for physiological over genetic adaptation; a preference for understanding the sources of variation rather than how this variation is sifted by the environment; a preference for explanations based on cooperation rather than conflict; a preference for time-scales of a few generations rather than much longer periods; a preference for theoretical revolution over theoretical evolution; and, a distaste for all, but the last, of these dichotomies.

Whether current trends in biology are seen as falling within a neo-Darwinian paradigm, a Lamarckian paradigm, or some synthesis of the two can thus be seen as a matter of personal preference. The rhetorical role of linking modern discoveries to Lamarck is clear. Lamarck was discredited by the Modern Synthesis. Therefore, if new discoveries support Lamarck, then there needs to be a radical reformulation of evolutionary theory. The opposing rhetorical maneuver is to deny a connection to Lamarck and argue that phenotypic plasticity, epigenetic inheritance, and the like, can be accommodated easily within existing theory and do not challenge reigning paradigms.

Differences of personal preference can be matters of indifference or can be fiercely disputed. A distinctive feature of debates about evolutionary theory is how often discussion resembles political argument. We take 'sides.' We want our side to 'win' and the other to 'lose.' We engage in 'spin,' the construction of straw-men, and selective and anachronistic quotation. The passion undoubtedly comes from fear that particular theories may have implications for the human condition or an indignation about favored theories being politically pigeon-holed.

My neo-Darwinian preferences should, by now, be clear to readers of this review, and I will not attempt a self-analysis that undoubtedly would be self-serving. Rather I will give my subjective impressions of the reasons why many people I have talked with, both in the general public and the scientific community, have a visceral attraction to Lamarckism and a visceral dislike of Darwinism. These reactions relate to the two aspects of natural selection: random variation and 'survival of the fittest.' A neo-Darwinian view, with its emphasis on chance and randomness in the origin of variation, is perceived as positing a world without meaning that is less attractive than a Lamarckian view in which organisms have agency in shaping their evolutionary destiny. Natural selection, with its reliance on differential survival and reproductive competition, is also perceived as bleak and harsh. The beauties of the human form are ascribed to the elimination of the slightly less perfect in lives that were nasty, brutish, and short. A consistent application of this view has led some prominent evolutionary thinkers to espouse eugenics (Haig 2003). But it is a view from which many recoil. Phenotypic plasticity and the inheritance of acquired characters seem to hold hope that we all can improve without processes of selection.

A neo-Darwinist would undoubtedly argue that ascribing the origin of purposeful agents in the world to a process without inherent purpose is intellectually satisfying. But this is a view that leaves many cold. It is not how they emotionally react to 'works of nature.' *ToL* finishes with a poem by Osip Mandelstam and I will finish with the final lines of one of Shakespeare's great sonnets:

Yet in these thoughts my self almost despising,
Haply I think on thee, and then my state,
Like to the lark at break of day arising
From sullen earth, sings hymns at heaven's gate;
For thy sweet love remembered such wealth brings
That then I scorn to change my state with kings.

The lark ascending has inspired poems by William Shakespeare and George Meredith, and music by Ralph Vaughan Williams. The display of the male skylark has been used to evoke selfless joy but a neo-Darwinist might describe the display as an honest, because strenuous, signal of quality made credible by the risk of being taken by a hawk. The lark is probably not bursting with joy, but exhausted and afraid. Shakespeare's and Meredith's transcendent metaphors could be seen as reflecting an erroneous view of the natural world. Does the striving of the lark have no higher end than showing-off to attract mates? Is there squalor in this view of life? When I observe a lark at break of day arising from an Oxford meadow, must the richness of the scientific vision impoverish the poetic image? Must the neo-Darwinist live in a disenchanted world?

Literature cited

Bowler, P.J. 1983. The Eclipse of Darwinism. Baltimore, MD: Johns Hopkins University Press.

Eshel, I. 1996. On the changing concept of evolutionary population stability as a reflection of a changing point of view in the quantitative theory of evolution. Journal of Mathematical Biology 34: 485-510.

Haig, D. 2003. The science that dare not speak its name. The Quarterly Review of Biology 78: 327-335.

Haig, D. 2007. Weismann rules! OK? Epigenetics and the Lamarckian temptation. Biology & Philosophy 22: 415-428.

Jablonka, E. and M.J. Lamb. 2005. Evolution in Four Dimensions: Genetic, Epigenetic, Behavioral, and Symbolic Variation in the History of Life. Cambridge, MA: MIT Press.

Romanes, G.J. 1888. Lamarckism versus Darwinism. Nature 38: 413.

Scott-Phillips, T.C., T.E. Dickins, and S.A. West. 2011. Evolutionary theory and the ultimate-proximate distinction in the human behavioral sciences. Perspectives on Psychological Science 6: 38-47.

Weismann, A. 1891. The significance of sexual reproduction in the theory of natural selection. In Essays upon Heredity and Kindred Biological Problems, Volume 1. Ed. by E.B. Poulton, S. Schönland, and A.E. Shipley. Oxford: Clarendon Press.

Weismann, A. 1893. The all-sufficiency of natural selection. A reply to Herbert Spencer. Contemporary Review 64: 309-338.

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