DARWINISM AND LAMARCKISM BEFORE AND AFTER WEISMANN: A HISTORICAL, PHILOSOPHICAL, AND METHODOLOGICAL ANALYSIS

by
Francis J. Cartieri
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This thesis was presented

by

Francis J. Cartieri

It was defended on

April 21, 2009

and approved by

David Denks, Professor, Philosophy

Jeffrey Schwartz, Professor, Anthropology

Peter Machamer, Professor, History and Philosophy of Science

Thesis Director: Sandra Mitchell, Professor and Chair, History and Philosophy of Science

ABSTRACT

Darwinism and Lamarckism before and after Weismann: A Historical, Philosophical, and Methodological analysis.

Francis J. Cartieri

Chair: Sandra D. Mitchell

When exploring the relationship between two reputedly competitive scientific concepts that have persisted, with modification, through time, there are three main features to consider. First, there are historical features of an evolving relationship. Just as a causal story can be reconstructed concerning adaptations in a complex system, an analogous story can be supplied for the historical contingencies that have shaped the organization and development of Lamarckian and Darwinian biological thought, and their interactions, over time. Second, there are philosophical and conceptual features to the relationship-- what is shared, what is not, whether two ideas inherently conflict or conditionally conflict, etc. Third, there are methodological features to the relationship—how do the theoretical concepts interact when in realistic operation? What are the benefits and constraints regarding their co-application? This project will explore the historical, philosophical, and methodological characteristics of the infamous Darwinian-Lamarckian dichotomy as characterized through Lakatos' Methodology for Scientific Research Programs, with the hypothesis that, once the respective evolutionary philosophies are generalized and the clutter of stigma removed, there is a large degree of compatibility to be found among them. The justification for this project derives from the recent resurgence of interest in Lamarckian phenomena and the stern, often vehement backlash that has greeted that interest. If biologists and philosophers both resist, or worse dismiss, Lamarckian suggestions on the grounds that they perceive them to undermine and conflict with Darwinian lines of thought, then that resistance may be unconstructive and misguided, should it be the case that, just as it was with Darwin's original conception of evolution, a more flexible, pluralistic view is plausible.

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I. INTRODUCTION

From the mid to late 19th Century, the dominant research program accounting for evolutionary phenomena was comprised of elements of Lamarck's Zoological Philosophy and Darwin's Origins of Species. Working scientists, and Darwin himself, took the presence of widespread variation and heritability of that variation to be an issue properly addressed only with appeal to the Inheritance of Acquired Characters (IAC) and the effects of use and disuse. The evidential climate of the time allowed and encouraged compatibility of Darwin's account and elements of Lamarck's account. When the two programs once again became distinct, it was not a result of their inherent incompatibility, but a result of the presentation of divisive new evidence, for which neither traditional Darwinian principles nor traditional Lamarckian principles could account. In reacting to the divisive evidence set, characterized by the Weismannian doctrine of the late 19th century, the dominant Darwinian research program produced two novel programs, each confining themselves to exclusive scientific niches and responding in distinct ways to the new evidence set. Reformulated as Neo-Lamarckism and Neo-Darwinism, the two research programs diverged in their development and application as long as the divisive evidence set continued to be held as fact by most biologists. In fact, in reacting to the Weismann doctrine, each new formulation took a position conceptually opposed to the other. On the Neo Darwinian side, the Synthesis served to rigidify the philosophy that variation is random with respect to the environment and genetic factors account for all aspects of heredity, making Natural Selection on heritable random variation the only force relevant in evolution. Neo Lamarckism, *confined primarily to the social sciences, paleontology, developmental biology and embryology, asserted that non-genetic factors contribute to development and development controls heredity, and as such, Inheritance of Acquired Characters and other non-genetic factors play a significant role in evolutionary phenomena. With the modern rejection of the original divisive evidence set, the two theoretical programs stand at a curious and ambiguous relation to one another. On the one hand, the two programs today continue to successfully account for various phenomena within their problem domains. On the other, their longstanding isolation and opposition has resulted in an apparent rigidity that disallows flexibility regarding points where the programs disagree. It will be the aim of this paper to make clear the conceptual relations between the two research programs of modern Darwinism and modern Lamarckism. It is my suspicion that a careful philosophical analysis will reveal more compatibility than incompatibility, with the recognition that the Neo-Lamarckian program offers a proximate explanation of the generation and maintenance of variation at biological levels of analyses that are lower than the discrete phylogenic individual upon which Neo Darwinism concentrates. This is not to say that every element of each program can be at once tacked on to the other with perfect harmony. Quite the contrary: the historical and logical analysis will serve to show exactly why this is not possible, and why there are areas of the two programs that are indeed contradictory to one another. However, that there are areas of significant overlap between the two is likely, and with the degradation of the causes for their logical incompatibility, the potential benefits of a more forgiving relationship between a Darwinian line of thought and a Lamarckian line of thought are many and promising.*

Methods

When exploring the relationship between two reputedly competitive scientific concepts that have persisted, with modification, through time, there are three main features to consider. First, there are historical features of an evolving relationship. Just as a causal story can be reconstructed concerning adaptations in a complex system, an analogous story can be supplied for the historical contingencies that have shaped the organization and development of Lamarckian and Darwinian biological thought, and their interactions, over time. Second, there are philosophical and conceptual features to the relationship-- what is shared, what is not, whether two ideas inherently conflict or conditionally conflict, etc. Third, there are methodological features to the relationship— how do the theoretical concepts interact when in realistic operation? What are the benefits and constraints regarding their co-application? This project will explore the historical, philosophical, and methodological characteristics of the infamous Darwinian-Lamarckian dichotomy as characterized through Lakatos' Methodology for Scientific Research Programs, with the hypothesis that, once the respective evolutionary philosophies are generalized and the clutter of stigma removed, there is a large degree of compatibility to be found among them. The justification for this project derives from the recent resurgence of interest in Lamarckian phenomena and the stern, often vehement backlash that has greeted that interest. If biologists and philosophers both resist, or worse dismiss, Lamarckian suggestions on the grounds that they perceive them to undermine and conflict with Darwinian lines of thought, then that resistance may be unconstructive and misguided, should it be the case that, just as it was with Darwin's original conception of evolution, a more flexible, pluralistic view is plausible.

II. CRITICAL HISTORY

"Our attitudes towards the great problems of biology are shaped by historical contingencies." –Raff, 1996

In this section, I will discuss the numerous transformations of Darwinian and Lamarckian lines of thought as scientists and philosophers of various domains adjusted to changing evidence sets over time. As the goal of this project is to assess the modern relationship between Darwinian thinking and Lamarckian thinking, we will need some structured description of just what delineates those modes of evolutionary thinking from one another. Of course, the difficulties in providing a non-arbitrary account of the transformations of Darwinism are many (Lennox 1995, Gayon 1995), and worse, the collection of ideas commonly referred to as "Lamarckian" is so loose and disjointed that they can hardly be said to comprise a rigid theory of evolution on their own. Despite these difficulties, there is a way in which Neo-Darwinism, in each of its fluctuating forms, remains Darwinian, through adherence to a core set of principles that may be construed as Darwinian. In the same way, formulations of Lamarckism differ widely, but can be understood as "Lamarckian" in that they adhere to a general mode of thinking about evolutionary problems. If we are to ascertain the level of conflict between a

Darwinian mode of evolutionary thought and a Lamarckian one, then it is at the level of the most general expressions of the philosophies that we must begin. For this purpose, Lakatos' notion of the *Research Program*[1] will be helpful; it may be used to zero in on the set of interrelated concepts that express the most essential and consistent elements of Darwinian and Lamarckian thinking, respectively.

A *research program* is a series of general concepts, theories or hypotheses that share a common 'hard core' of general assumptions about the domain of problems, or *problem domain*, to be explained, but which are individuated in terms of their particular sets of peripheral, auxiliary hypotheses; these are called the '*protective belt*.' The hypotheses, assumptions, and observations of the protective belt support the hard core. They may be refined, adjusted, and replaced over time without compromising the identity of the research program itself, so long as the hard core remains unchanged. This is Lakatos's *negative heuristic*: a methodological stipulation that the hard core must not be fundamentally modified. As Lakatos explains, "the negative heuristic forbids us to direct the *modus tollens* at this 'hard core'" (Lakatos, p. 135). Instead, attempts at falsification and testing are to be redirected at the protective belt of auxiliary assumptions that are required by the hard core of the program. This is the *positive heuristic*—it tells researchers how to augment the general program through its protective belt, without compromising its essential character. Through modification of the protective belt, a research program may increase the accuracy and scope of its predictions and accounts of

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[1] I acknowledge that there are alternative methods for characterizing scientific history in Kuhn, Laudan, Popper, Feyerabend and others. My choice of Lakatos' MSRP is motivated by its ability to account for the operation of several competing programs at once, its simplicity, and for it's rational for the continued support of degenerative programs in the history of science, as Lamarckism most certainly has been.

its problem domain(s), thereby achieving *progressive* status. A program that fails to do this is *degenerative*. So, we also have a guide for judging the relative success of research programs with relation to each other—more progressive programs are favorable to degenerative, or less progressive, programs (p. 137). However, it should be noted that a degenerative program may again become progressive, so it is not irrational to remain committed to a degenerative research program (p. 155). This point is partially why it makes sense to evaluate Lamarckism as a research program—it had become degenerative at various points in history, followed by brief periods of progressive development. Where Popper would have us regard the Lamarckian position as falsified by *modus tollens*[2] (and disregard it), Lakatos' MSRP suggests only that it may be less favorable than a related progressive program, though it would not be irrational to continue to pursue a degenerative program, because the *modus tollens* may only imply the falsification of some auxiliary hypotheses, rather than the hard core of the program.

For an example, over time the Aristotelian hard core of an earth-centered universe and perfect circular orbits had to be burdened with many ad hoc hypotheses to account for ellipses, variable velocities, retrograde motion, etc., and it became degenerative. It was replaced by a program with the same problem domain, but characterized by a

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[2] This falsification strategy implements the modus tollens relation of deductive logic:
-If P then Q
-Not Q
-Therefore, not P

Since modus tollens is a valid deduction argument form, it is rational to reject the conclusion "not P" only if one can show that one, or both, of the premises are not true. Applications of this falsification strategy are widespread within science, even in the early stages of its development. Aristotle, for example, dismissed the suggestion of Herodotus that female fish conceive by swallowing the milt produced by males. He noted that if Herodotus's hypothesis is true then there is a passageway from mouth to uterus. Aristotle maintained that dissections reveal that there is no such passage. (Popper, Karl, *The Logic of Scientific Discovery*, 1954)

Copernican 'hard core' with Kepler's elliptical information as part of the protective belt, and this program was far more progressive and less ad hoc—it competed with and eventually replaced the Aristotelian program. Similarly, we can track the development of the relationship between Darwinism and Lamarckism by characterizing them as research programs, identifying their respective problem domains, hard cores, and protective belts as they have changed over time. In doing so, it should become clear in what way the programs relate to one another, compete, contradict, and share with each other.

Certain periods in history have seen more or less friction between the two programs, and the following sections will reveal the states of the two programs at those particular moments when the relationship between Lamarckism and Darwinism shifts: 1) the relation between both original programs, 2) the period of transition (Neo Lamarckism and Neo Darwinism are created) characterized by Weismann's doctrine and Mendelian heredity, 3) the state of the programs after they are isolated to different problem domains, and 4) the state of the programs today, given a "porous" Weismann barrier. I will begin with the research program initiated by Lamarck, as it was introduced half a century before the Darwinian research program.

THE DEVELOPMENT OF THE COMPLETE LAMARCKIAN PROGRAM

By 1815, Jean-Baptiste Lamarck had articulated what he believed to be "a truly general theory, linked everywhere in its parts, always consistent in its principles, and applicable to all the known data." This "truly general theory" is the original Lamarckian Research Program. It was nothing less than the union of a wealth of empirical observations of the natural world (empirical hypotheses of the protective belt) and a guiding philosophy of life (general assumptions of the hard core) that accounted for a large problem domain: “the source of existence, the manner of being, the faculties, the variations, and the phenomena of organization of the different animals” (Lamarck, ZP, p. 184).

Though Lamarck had established himself as a master systematist rivaling Linnaeus among his own contemporaries, he considered his work in nascent biology and evolution (incidentally, Lamarck actually coined the term ‘biology’) to be his most difficult, ambitious, and ultimately, his most important contribution to human understanding (Lamarck, 1809). However, Lamarck’s *general theory* was almost universally ignored (Corsi, p. 207); at best, he faced polite indifference, and at worst, outright slander and ridicule (Madaule, p. 13). From the very outset of its publication, Lamarck’s *Zoological Philosophy* was repeatedly misinterpreted, his ideas misquoted, and his name misappropriated. Unfortunately, the distortion of his ideas did not cease upon Lamarck’s death--even his academic eulogy, tragically written by his adversary Georges Cuvier, served to confuse and malign Lamarck’s ideas on the evolution and organization of nature (Cannon, 1959). The reception of Lamarck’s program has special relevance because Darwin’s notion of Lamarck’s general theory was largely secondhand (most notably from Lyell). He did not take it to be a viable program that stood or fell as one whole, but a collection of independent suppositions, some of which he incorporated into the protective belt of his particular research program, others he simply rejected. I will discuss this further when considering the Darwinian research program.

Lamarck was inspired by the successes of Newton in providing a unified scientific account of the motion of heavenly bodies and earthly motion in general; he hoped to find similar success in accounting for the complexity of all biological life. In grand fashion, he hoped to find and describe nature's plan (Glass, 1959). Particularly, Lamarck stressed that there is an obvious trend of increasing complexity among living things, and that this complexity was derived over time during the history of life, not through special creation events. Just like the laws governing the motion of planets and stars, Lamarck assumed that there must be active properties and plans that guided, and continue to guide, the evolution of life-forms, resulting in the natural and fine gradations observed by himself and others of his time (Jordanova, 1984). Lamarck, it must be noted, had not restricted his professional analyses to living matter; he published widely on geological and marine history as well (Bowler, 1989). From his observations in geology, he recognized that the earth, though having undergone gradual and sometimes sudden changes over its long history, had not become more complex. Thus, he reasoned, because the state of the organic world is more complex than it was in the past, living matter must tend toward the more complex via inherent guiding properties (contra directionless geological change). He was perhaps no less influenced by social, political and economic theories than by his own observations of the natural world. For example, Lamarck was known to take frequent walks with Jean-Jacques Rousseau, and in various letters it is apparent that he applied some of Rousseau's political philosophy to the natural world (and perhaps vice-versa, to be fair) (Madaule, 1982). From the ideological French climate and his observations of the natural world and his phylogenic series, Lamarck developed a two-factor approach to account for the problem domain of present biological organization and successive biological change, consisting of 1) the *natural inherent progress* of organic development from simple to complex forms and 2) the modification of this progress by *constraining external circumstances* resulting in creative adaptations to changing environments (Burkhardt, 1977).

By 1809 in his Zoological Philosophy, Lamarck reports on the natural progress of evolution directed by nature and the distorting and random effects of accidental circumstances (the environment): “The state in which we now see animals is on the one hand the product of the increasing *composition* of the organization, which tends to form a *regular gradation*, and on the other hand that of the influences of a multitude of very different circumstances that continually tend to destroy the regularity, the gradation of the increasing composition of organization“ (Lamarck, 1809; not my emphasis). This two factor approach to the problem domain of his research program forms the hard core of the Lamarckian Research Program.

Another important tenet of Lamark’s thought involved the subordination of certain biological features in relation to others (Burkhardt, 1977). He attributed more superficial changes, like those that distinguish species from one another, to the influence of circumstances on evolution (factor 2 in chart below), and the development of the more essential and incorporated features (organs, blood types, etc.) to the inherent properties of life, sometimes called “the power of life.” This means that the evolution of structures such as the eye and nervous system were the result of the properties of the cellular fluids of life (complexifying force), while features such as sexual dimorphism or tooth structure were primarily determined by alterations of habit in response to changing circumstances (adaptive force). These two forms of explanation were to go on to form the protective belt of Lamarck's research program.

An additional element of Lamarck's problem domain, that of the presence of fossils of living things no longer on earth, demanded an explanation by the 1800's. Where the catastrophists appealed to biblical disasters as evidence of both geological change and the disappearance of older animals (Hodge, 2008), Lamarck developed the view that organisms are highly mutable with respect to their changing environments; organisms possessed a natural inherent tendency to increase in number, size and complexity, but would, in adapting to changing circumstances, cause alterations to their forms through new habits and behavioral patterns. The great flexibility Lamarck attributed to living things caused him to deny the regular occurrence of extinction events—we don't see animals in the fossil record because they have transformed into other creatures over time.

In 1809, Lamarck was introducing a fundamentally new research program composed of a general problem domain, a two-component 'hard core,' and a set of auxiliary hypothesis that, when conjoined with the hard core, accounted for the phenomena of the problem domain. The problem domain—the general set of phenomena to be addressed by the program—can be taken to be general organic change over time (macro-evolution) and local adaptation (micro-evolution). Because it appears that the problem domain is naturally divided into two general problems, the original, circa 1809, "hard core" of the program also had two general components: a complexifying force (*Le* *pouvoir de la vie*) and an adaptive force (*L'influence des circonstances*) that have resulted in the regular and specialized gradations among species, respectively. He summarizes the hard core of his program in *Zoological Philosophy:*

" Nature, in producing successively all the species of animals, beginning with the most imperfect or most simple in order to end her work with the most perfect, has gradually made their organization more complex; and with these animals spreading generally throughout all the habitable regions of the globe, each species received from the influence of the circumstances in which it is found the habits now recognized in it and the modifications of its parts that observation shows to us…" (ZP 1809)

Finally, the protective belt of Lamarck's theory is a collection of more specific hypotheses that apply the hard core to empirical cases, and allow for the operation of the hard core to real phenomena. Lamarck's four laws of evolution, reproduced below, are part of the protective belt of his program and when taken together, serve as a mechanism for localized adaptation.

Four Evolutionary Laws (from his Natural History of Invertebrates), 1815:

1. Life by its own forces tends continually to increase the volume of every body that possesses it, as well as to increase the size of all the parts of the body up to a limit which it imposes upon itself.

2. The production of a new organ in the body of an animal results from a new need arriving unexpectedly and continuing to be felt, and from the new movement which this need initiates and maintains.

3. The development of organs and their power of action are always proportional with the use of these organs.

4. Everything that has been acquired, delineated, or altered in the organization of individuals during their life is preserved by generation and transmitted to new individuals proceeding from those which have undergone these changes.

In addition to the above "four laws," the protective belt of the Lamarck's program requires some mechanism of heredity that supports the four laws and the hard core. Lamarck assumed that the Inheritance of Acquired Characters (IAC) was allowed by the modes of heredity that applied to his problem domain, though he made no effort to develop one himself (as Darwin did with pangenesis), noting merely that offspring always tend to resemble their parents. One adjustment that was made within the protective belt served to deal with the presence of very simple forms of life. Lamarck's hard core predicts that living matter tends to continually develop towards complexity. If the earth is sufficiently old, we should not see extremely simple forms of life, as they should have developed into more complex forms. The notion of *spontaneous generation* was an auxiliary hypothesis that allowed for the continual creation of simple forms of life. Notice, the *modus tollens* is directed at the protective belt, not the hard core of

Lamarck's program. Specifically, the hard core (complexifying force) predicts widespread complexity, but observation shows the presence of very simple life forms, counter to the prediction of the hard core. However, an auxiliary hypothesis, continuous spontaneous generation of simple life forms, accounts for the anomalous observation, and protects the hard core from falsification, because the hard core is always associated with a set of auxiliary hypotheses, and these are to be blamed for incongruence between a program's predictions and actual observation.

So to summarize:

Lamarckian Research Program before Weismann

Problem Domain: Organic change over time and local adaptation.

Hard Core: 1) There is an inherent force in living matter that results in a progression from simple to complex structure: a tendency toward progressive development. 2) Organisms habits and forms are sensitive to modification by environmental circumstances: adaptation occurs via IAC.

Protective Belt: Mechanism of heredity that allows for IAC, blending inheritance, effects of use/disuse, spontaneous generation, very long timescales, etc.

THE DARWINIAN PROGRAM BEFORE WEISMANN

Darwin began writing manuscripts for the *Origin* at a time when the notion of species mutability and evolution at large was gradually becoming more acceptable (Hodge, 2008). There was, however, no generally accepted account in place of how evolution might proceed, at least in Britain, that researchers could work under. While Lamarck had forwarded a complete research program accounting for the development and organization of life over fifty years earlier, his theory had suffered from a lack of immediate positive reception, critical failure, and numerous distortions (Cannon, 1959). The result of his program's reception, and subsequent misrepresentation in Britain, would have major effects on the development of Darwin's research program.

Charles Lyell's work had a profound impact on Darwin's thinking (especially his requirement that historical processes should be explained using extant processes), and the two became close acquaintances. It was the case that Darwin, along with many other English naturalists, became familiar with Lamarck's ideas through Lyell and his *Principles of Geology*. That is to say, they became familiar with Lyell's Lamarck, not Lamarck's Lamarck. In the second volume, he characterizes what he calls "Lamarck's theory of the transmutation of species" in quite disparaging terms. He says of Lamarck's program, for example, that

"Lamarck talks of the efforts of 'internal sentiment,' 'the influence of subtle fluids,' and the 'acts of organization,' as causes whereby animals and plants may acquire *new organs*, he gives us names for things, and with a disregard to the strict rules of induction, resorts to fictions, as ideal as the 'plastic virtue,' and other phantoms of the middle ages."
(PG vol. II, p.8)

Besides his charge that Lamarck's program ignores "the rules of induction," Lyell repeatedly observes that there is no positive evidence to support the mechanisms required by Lamarck's research program: "We point out to the reader this important chasm in the chain of the evidence… but the plain truth is, that there were no examples to be found." He directly attacks the Lamarckian hard core as ungrounded, "…gratuitous assumption…of a point so vital to the theory of transmutation, [as to be] unpardonable on the part of its advocate." (p. 9) While Lyell thought the Lamarckian hard core to be ungrounded, he noted that its implications for evolution, "however staggering and absurd it may seem, is logically deduced from the assumed premises," and endeavored to show that, even granted Lamarck's ungrounded assumptions, his program fails as a viable theory of transmutation.

However, Lyell certainly did not initially accept *any* account of the transmutation of species, though he admitted some natural flexibility to them (p. 18). Despite this, he argues against the unlimited flexibility that he claims Lamarck to endorse, and emphasizes that species are real entities with limits to manipulation. (p. 35) Later, in letters to Darwin after the publication of the *Origin*, Lyell would reverse his position, noting: “When I came to the conclusion that after all Lamarck was going to be shown to be right, that we must `go the whole orang,' I re-read his book, and remembering when it was written, I felt I had done him injustice.” (Letter 4041 — Lyell, Charles to Darwin, C. R., 15 Mar 1863).

The injustice, of course, had already been committed during the formative period of Darwin’s research program, and as such, Darwin did not consider Lamarck’s original program as either a viable account of its problem domain, or even as one inseparable whole program. Given Lyell’s account of Lamarck’s program, Darwin was able to incorporate a major element of the Lamarckian program into the protective belt of his own research program. This was possible because the original “hard core” of the Lamarckian program had ceased to be protected, as it were, by its protective belt, both because there was a lack of supporters for the whole program in Britain, and because two supposed implications of the Lamarckian program—spontaneous generation and no extinction—were taken to be false, and no modified hypotheses were given to replace them in the protective belt. Having developed a sense that Lamarck’s initial program was insufficient as an account of its problem domain from Lyell, Darwin’s program subsumed the most viable elements from the Lamarckian hard core and protective belt into the protective belt of his own program, in support of a new, distinctively Darwinian hard core:

Darwinian Research Program before Weismann.

Problem Domain: Organic change over time and local adaptation.

Hard Core: Species are linked through common ancestry: changes in species are primarily due to Natural Selection acting on heritable variation among populations of individuals.

Protective Belt: Mechanism of heredity that allows for production and maintenance of variation and IAC, geological distribution of species, blending inheritance, effects of use/disuse, IAC, ubiquitous variation, Struggle for Survival, relations between species, etc.

Darwin's program adequately described extinction as an inevitable result of the selection of better-adapted varieties over more poorly adapted varieties in life's Sturggle for Existence. It also anticipated an evolutionary structure as primarily that of a randomly branching network, not one of inherent progress from simple to complex arising from the continuous generation of simple life forms, as Lamarck's program did. The above generalization of the two research programs should make it plain that their hard core assumptions deeply conflict with one another. The programs share identical problem domains, but make fundamentally different, inflexible assumptions about them. Lamarck's hard core assumes that there is force inherent in nature that results in increasing complexity, and that complexifying force is primarily responsible for the observed organization of the taxa; Darwin's hard core assumes quite the opposite. The primary force in generating the observed taxa is Natural Selection, a blind and stochastic process, and there is no "built in" tendency in individuals to progress from simple to complex forms. Selection may as well favor more simple forms, and this is why we see the preservation of very simple species—not because they are continually arising via spontaneous generation. At first glance, it may seem curious that Darwin's program incorporates elements of Lamarck's, when it is evident that their hard cores directly conflict with one another. However, the original Lamarckian program, with its two-component hard core, was not active in Britain when Darwin wrote the *Origin*, and we may assume Darwin shared Lyell's sentiment regarding the insufficiency of Lamarck's program at large:

"…if species were not created separately, they must have descended from other species: & I can see nothing else in common between the Origin & Lamarck. I believe [Lamarck's] way of putting the case is very injurious to its acceptance; as it implies necessary progression & closely connects Wallace's & my views with what I consider, after two deliberate readings, as a wretched book; & one from which (I well remember my surprise) I gained nothing" (Letter 4038 — Darwin, C. R. to Lyell, Charles, 12–13 Mar [1863]).

So Darwin was dealing with what he perceived to be a dead research program that took as its hard core opposing assumptions to his own program's. However, he could excise ½ of Lamarck's hard core and subvert it to a supporting role within the protective belt of his own research program, because the notion of IAC and use/disuse helped to deal with the problem of blending, the disappearance of useless organs, and other phenomena within the problem domain of his program. Doing so did not risk reviving the entirety of the Lamarckian program (which would indeed have been incompatible with Darwin's program), because the part of the Lamarckian hard core relating to IAC was not inextricably bound up with the assertion that life is guided by a complexifying force. Thus, support for IAC within Darwin's program did not mean support for the entire Lamarckian program as it had been originally conceived.[3]

As has been said, the ½ of the hard core that Darwin appropriated from Lamarck's program was perceived by Lamarck himself to be an inherently unguided process—unpredictable fluctuations in the environment for Lamarck resulted in specialized adaptation and "degradation" of nature's organized procession towards perfection. The complete Lamarckian program was particularly interesting because it contained two seemingly *opposing forces*—Darwin appropriated the environmentally driven adaptive force as it conveniently obeyed the powers of Natural Selection. Insofar as Lamarck's *L'influence des circonstances* is not taken to be universal for every single trait in every single individual, it serves only to *aid* Natural Selection within the protective belt

[3] The succession of the Copernican research program over the Ptolemaic program bears a good deal of resemblance to the succession of the Darwinian program over the Lamarckian program. The Copernican program arrived at a time when the Ptolemaic was incorporating increasing numbers of *ad hoc* hypotheses to account for phenomena such as equinoxes and inaccurate predictions of planetary position. The Copernican system incorporated the assumption of circular motion of the Ptolemaic hard core, but asserted a sun centered system as a better account observed changes in the positions of celestial bodies—the problem domain shared by both programs—and offered better predictions with fewer assumptions and a simpler overall structure. (Kuhn, p. 68)

Darwin's research program. In decomposing the Lamarckian program into two separate components, one contradictory to Darwin's program and the other supplemental, it clear how the half characterized by IAC persisted and flourished within the Darwinian program.

One important implication of Darwin's incorporation of ½ of the Lamarckian program was his own program's inheritance of the same hereditary requirements as Lamarck's program. A mechanism of heredity was implied by the Darwinian program that allowed for environmental influences to affect germ material (IAC and use/disuse), for blending, and for the production and maintenance of widespread variation among individuals. Darwin's provisional theory of heredity, pangenesis, satisfied all these requirements, though with little evidence to support it save the success of his own program that supported its existence. Pangenesis occupied the space in Darwin's research program reserved for a mechanism of heredity that allowed for the hard core propositions of his program. Because pangenesis was also situated alongside the hypothesis of adaptation via IAC, the hypothesis of pangenesis accommodated the transmission of acquired characters. It accomplished this by postulating that all body cells continually shed tiny "gemmules" that concentrate in the reproductive center of the body before fertilization occurs. Because the cellular environment affects, to some extent, which gemmules are shed, the environment plays a role in the composition of the new individual (Gould, p.166). As Weismann would later show, removal of pangenesis and IAC from the protective belt of the Darwinian program would not compromise its identity. Such an event would, however, force those that still accepted IAC as part of the hard core of their *specific* disciplines (social evolution, psychology, embryology, developmental biology, etc.) out of the Darwinian research program.

Another conclusion that must be drawn at this stage is that, if only ½ of the Lamarckian hard core is preserved and the other ½ is rejected, then we have the destruction of the original Lamarckian research program itself. And this is indeed the historical case. That the complete Lamarckian program contradicts the Darwinian program has been shown in principle—but at this stage in history, *only an active and complete Lamarckian program contradicts the Darwinian program*. Neo Lamarckism, which evolved from a synthesis of the remaining ½ of the Lamarckian hard core and the Darwinian concepts, is an entirely different beast, and its relation to the next instantiation of Darwinism, instigated by Weismann, will now be examined.

WEISMANN AND THE CREATION OF A NEW LAMARCKIAN PROGRAM

Any discussion of the development and relations between Darwinian and Lamarckian ideas requires an understanding of August Weismann and his theory of the continuity of the germ plasm. Where the provisional hypothesis of pangenesis served to align Darwin's hard core and the Lamarckian elements within the protective belt of his research program, Weismann's theory of the continuity of the germ-plasm would represent its near total inversion. Weismann asserted that 1) hereditary material resides exclusively in "immortal" germ cells, and 2) that germ cells are fundamentally distinct from the somatic cells:

"…A marked antithesis exists between the substance of the undying reproductive cells and that of the perishable body cells. We cannot explain this fact except by the supposition that each reproduction cell potentially contains two kinds of substance, which at a variable time after the commencement of embryonic development, separate from one another, and finally produce two sharply contrasted groups of cells." (Weismann, Essays Upon Heredity, p. 74)

If there is a fundamental barrier between the cells that are subject to environmental influences (somatic cells) and the cells that give rise to the next generation (germ cells), then IAC is theoretically impossible in any organism where the continuity of the germ-plasm is taken to be true, because somatic adaptations cannot be transmitted to the protected hereditary material. Just how universal the soma/germ-line separation is taken to be in the organic world has significant consequences for the modification of the Darwinian program. If soma/germ separation is universal, as Weismann argued, then IAC cannot play a role in explaining the Darwinian problem domain of biological adaptation, and further, pangenesis must not be correct. If soma/germ-line separation is *not* a universal feature of organic life, then IAC remains as a possible explanation of adaptation.

Weismann's *Allmacht*, an argument for the "all sufficiency of natural selection," derives from the assumption that soma/germ separation is universal, and involves a *modus tollens* argument directed at the IAC auxiliary assumption within the protective belt of the Darwinian research program. If we recall that the IAC assumption in the Darwinian program is the remnant ½ of the original Lamarckian hard core, and that it was responsible for accounting for local adaptation within that program, we can better understand why Weismann argued that the exclusion of IAC implied the universal truth of Natural Selection regarding an explanation of adaptation:

"For there are only two possible *a priori* explanations of adaptations for the naturalist—namely, the transmission of functional adaptations and natural selection; but as the first of these can be excluded, only the second remains… We are thus able to prove by exclusion the reality of natural selection… Once it is established that natural selection is the only principle which has to be considered, it necessarily follows that the facts can be correctly explained by natural selection" (1893, pp. 336-7).

At this point in time, only Wallace and Weismann argued that natural selection was the *only* explanation required to account for evolutionary phenomena. Their position represented a rigidifying of the Darwinian program, in two major ways. One, the exclusion of IAC from the protective belt means that all evolutionary phenomena under the problem domain of the program must be explained through Natural Selection alone. Second, the incorporation of Weismann's doctrine *into* the protective belt of the program means that evolution is to be understood as the operation of natural selection on discrete individuals, because "…if not all cells contain heritable material, selection is necessarily on the individual, not on the cells or their constituents." (Buss, p. 8) In light of these limitations, many researchers simply rejected the universality of Weismann's rules, and continued to employ IAC as a valuable part of their more specific research programs.

This rejection was the case for some researchers, such as embryologists, because they saw that the particular cellular environment and cellular orientation determines the structure and organization of the developing individual. For others, such as botanists, their observations of plant development and reproduction did not agree with Weismann's assertions—any plant cell can potentially become a new individual; the notion of an immortal germ line simply does not hold for botany. Still more researchers recognized the absence of any means of generating the variation that Darwin's theory required, without IAC, if germ material is constant and un-altered across generations.

In fact, Weismann was quite wrong about heredity in most respects. All cells in fact contain the material of heredity, DNA. Germ cells can sometimes be produced from somatic cells, even after an animal is neutered. Plants can reproduce new individuals from nearly any part—there is little or no sequestering of independent germ cells. Bacteria can incorporate hereditary material from the environment that is reproduced in subsequent generations.

Despite all this, the implication of Weismann's germ/soma distinction was gradually incorporated into the Darwinian program's protective belt. The implication—that the hereditary material that gives rise to the next generation is protected from the influence of features of the ontogeny that it produces—is called the Weismann barrier. It excludes Lamarck's adaptive force from any program that takes the Weismann barrier seriously, as does the Neo-Darwinian program characterized by the synthesis of Mendelian genetics, Natural Selection, and Weismann.

<u>Neo-Darwinian Research Program</u>

Problem Domain: Macroevolution and Adaptation (microevolution).

Hard Core: Species are linked through common ancestry: changes in species are primarily due to Natural Selection acting on heritable variation among populations of individuals.

Protective Belt: Mendelian genetics, Weismann's barrier, Mutation, Population genetics

The ½ core of the original Lamackian program that was divorced from the Neo Darwinian protective belt did not simply disappear. Forced out of Neo Darwinism by the Weismann barrier, it was taken up by researchers in a diverse set of fields that felt that selection on random heritable variation alone was not enough to account for all adaptation:

"The idea of the inheritance of acquired characters had great breadth of appeal in the last decades of the nineteenth century and the early decades of the twentieth century. This appeal cut across both national and disciplinary boundaries, and it drew support from philosophical and social considerations as well as scientific ones…The Lamarckian position was supported in England, France, Germany, Austria, Switzerland, Italy, Russia, and the United States by embryologists, paleontologists, physiologists, bacteriologists, and plant geographers. It seemed to fit well with the embryologist's assumption that ontogeny recapitulates phylogeny, with the paleontologist's fossil sequences that seemed to display the accumulated effects of use and disuse, with the physiologist's interest in causal rather than statistical relationships, with the bacteriologist's understanding of the bacterium's adaptation to environmental change, and with the plant geographer's data on the geographic variation of forms. In a more straightforward manner than Darwinism, Lamarckism also seemed capable of explaining the degeneration of useless organs, correlated variation, and the origin of various kinds of instinctive behavior." (R. Burkhardt, Lamarckism in Britain and the United States, p. 346)

Until about 1920, Neo-Lamarckism was a viable research program, at least in the United States, which took as its problem domain the same phenomena as had Darwin's original program. One of the program's most interesting features was its incorporation of both Natural Selection on heritable variation, and Lamarck's adaptive force as its hard core. Despite establishing a school dedicated testing IAC, the American program failed to provide singular proof of IAC in operation (Cook, p. 434). With the rise of Mendelian genetics and its synthesis with Natural Selection, support for IAC would continue to dry up unless a viable mode of heredity was found to allow for its operation. As it happened, no viable hypotheses were presented, and Lamarck's adaptive force gradually fell from favor. "Rather than refutation, it faced a gradual loss of interest as the new science of genetics began to show the achievements that were possible with an alternative concept of heredity" (Bowler, p. 76) For its part, after a brief period of turmoil, characterized by the DeVries mutation controversy and the limitations of Weismannian heredity, the modified Neo Darwinian program had become a highly progressive research program with respect to its problem domain, while Neo Lamarckism still lacked a viable mechanism for IAC. As such, it was necessarily restricted to domains where the Weismann barrier does not play a major role. Most notably, this involves developmental biology: “After the publication of Darwin’s *origin of Species*, but before the general acceptance of Weismann’s views, problems of evolution and development were inextricably bound up with one another. One consequence of Weismann’s concept of the separation of the germ line and soma was to make it possible to understand genetics, and hence evolution, without understanding development.” (JM Smith, Evo and Theory of Games, p. 6) Developmental biologists concerned with how an individual develops saw little value in the synthesis, which can make no comment on differences among developing cells and the effect of their environments. As C.O. Whitman put it, “We are no better off for knowing that we have eyes because our ancestors had eyes. If our eyes resemble theirs it is not on account of genealogical connection, but because the molecular germinal basis is developed under similar conditions” (Whitman, p.7) The Neo Lamarckian program presupposes the importance of the link between cellular environment and developmental adaptations, and as such it was well suited to that problem domain.

Neo-Lamarckian Research Program

Problem Domain: Development, cultural evolution, learning

Hard Core: Organisms habits and forms are sensitive to modification by environmental circumstances; IAC.

Protective Belt: Reverse Transcriptase, EIS’s, the Baldwin Effect, etc.

By the mid 20th century, the Neo Lamarckian program and Neo Darwinian program had become compatible insofar as they had taken as their problem domains two exclusive areas of phenomena. This exclusivity was caused by the union of the Weismann barrier and Mendelian genetics, which implied that if IAC occurs, it must occur in the absence of a Weismann/Mendel system of heredity. As such, the Neo Lamarckian program "budded off" of the larger Darwinian program when Weismann/Mendel were incorporated into the protective belt of the Darwinian program. The problem domain of Neo Lamarckism has been restricted to those areas left out of the modern synthesis, most notably developmental biology.

As long as the Weismann barrier is assumed to be absolute, conflict between the Neo Lamarckian program and the larger Neo Darwinian program is impossible, as their problem domains cannot overlap. However, it is becoming increasingly apparent that the Weismann barrier is not absolute, that genetic inheritance is not the only means of inheritance, and that IAC may play a significant role in evolution. If the Neo Darwinian protective belt is not modified to accommodate these developments (to be discussed below), it risks becoming a degenerative program. However, the notion that some concept is "Lamarckian" tends to immediately disallow its consideration under the Neo Darwinian program, due in large part to a stress on what Popper would refer to as a competitive dichotomy, and that dates back to Lyell's treatment of the original Lamarckian program, and more significantly, Weismann's *allmacht* arguments asserting that selection and IAC are mutually exclusive. Below, I will examine the current nature of the Lamarckian-Darwinian dichotomy in light of the recent resurgence of interest in

Lamarckian adaptation. Following this, we can attempt to answer the question: *what are the implications of a "porous" Weismann barrier for the Neo Darwinian/Neo Lamarckian dichotomy?*

III. THE MODERN DICHOTOMY

The failure of those working under the American Neo-Lamarckian research program to demonstrate IAC or to produce a viable mechanism of heredity seemed to confirm the Weismann barrier, and resulted in the limitation of that program's problem domain to those areas of biology that were not properly addressed through the Neo Darwinian program. The subsequent lack of conflict between Neo Darwinism and any other evolutionary program has resulted in what Karl Popper has called "a too dogmatic adherence to Darwinism" (Popper, Evo Epistemology, p. 85). "Too dogmatic" is a negative accusation because Popper's notion of healthy science, as well as that of Kuhn and Lakatos, involves competition among research programs. "*The history of science has been and should be a history of competing research programmes (or, if you wish, 'paradigms'), but it has not been and must not become a succession of periods of normal science: the sooner competition starts, the better for progress"* (Lakatos, p.155). Seeing no active competitive research program to challenge Neo Darwinism, Popper has suggested a reconsideration of Lamarckian lines of thought, despite his belief that "…the Lamarckian line… seems to have been mistaken. Yet it may be worth while to speculate about the possible limits to Darwinism; for we should always be on the look-out for possible alternatives to any dominant theory" (Popper, Evo Epistemology, p.85). It is obvious that Popper views the “Lamarckian line” as a competitor to the Darwinian program. He is not alone. More than this though, Popper suggests that the Neo Lamarckian program represents an *alternative* to the dominant program, Neo Darwinism, which is a good deal stronger than suggesting that they are *competitive*. Two programs that are competitive must both be trying to explain some of the same things, surely. Their explanations must also differ in significant ways. However, two competitive programs are not necessarily *alternatives*, which would imply that one program could totally occupy the explanatory space of the other. Rather, they might only compete over a small overlapping problem domain, despite generally accounting for different phenomena. The two programs are perhaps alternatives with regard to the specific overlapping area of their problem domains, but they are not alternative research programs in general. In his *Allmacht*, Weismann asserted that there were only two possible options for explaining adaptation, and that they were *alternative* options: a competitive dichotomy. For him, the falsity of IAC implied the necessary truth of Natural Selection. Competitive relationships are not usually like this. Arguments for the unit of selection are often competitive with one another, but denying that selection does not occur on the group does not imply that selection must occur on the individual. Moreover, group selection theory could never *replace* individual selection theory, because group selection could never explain all the phenomena that individual selection explains—they are competitive with respect to particular problems, yes, but they are not alternatives with respect to the aggregate of both their problem domains. The distinction being made here is very important, because the overwhelming convention is to regard the Neo Lamarckian program as an alternative to Neo Darwinism. If a Neo Darwinian who thinks this way is confronted with a claim labeled as "Neo Lamarckian," it is no small wonder that she would resist its acceptance quite vigorously, because the implication of Neo Lamarckism being true could mean the replacement of her program by another. I believe this type of reaction, if misguided, does harm to the progress of biological science. Therefore, we should be sure to properly understand the relationship between Neo Darwinism and Neo Lamarckism today. In general, two research programs can be related in three different ways:

1) Non-competitive: their problem domains do not overlap.
2) Competitive, non-alternative: their problem domains share some overlap, but neither program could totally occupy the explanatory space of the other.
3) Competitive, alternative: the problem domain of at least one of the research programs could totally occupy the explanatory space of the other.

If we look back to my rationalized history of Darwinian and Lamarckian programs, it is interesting that the nature of their competitive relationship has dramatically changed over time. The original Lamarckian program and the original Darwinian program were *competitive alternatives*—they both shared the same problem domain and made opposing explanations for it. In fact, they were incompatible, because their hard cores directly contradicted one another: the complexifying force of Lamarck's hard core suggests an inherent tendency to a specific end—complexity, where Darwin's hard core assumes no inherent direction to evolution, only the effects of Natural Selection on heritable variation. Without the complexifying force, Lamarck's hard core is left only with his adaptive force, which of course Darwin incorporated into the protective belt of his own program. The Darwinian program and the ½ Lamarckian program were competitive in the sense that Natural Selection and IAC can both describe adaptation, but Darwin viewed IAC, as Lamarck did, as a secondary mechanism responsible for only some instances of adaptation.

Weismann's Neo Darwinian program takes all macro and micro-evolution as its problem domain, and asserts that *only* Natural Selection explains that domain. The Neo Lamarckian program of the same period competed to explain the same problem domain, but asserted that IAC plays a significant role in explaining adaptation. The two are thus competitive alternatives—they share the same problem domain but their explanations make opposing assumptions.

Following the acceptance of Weismann's barrier and Mendelian heredity, the two programs became non competitive, because they ceased to share any significant area of overlap. They were compatible only because they were explanatorily independent to one another.

Now, if it is the case, as Popper and most others believe, that the two programs are competitive alternatives, then they must *at least* share some area of overlap with respect to their problem domains. The widespread acceptance of Weismann's barrier makes competition impossible, confining Neo Lamarckism to its own exclusive domain. So, it must first be established that conditions today are such that the Neo Lamarckian program can overlap with some of the Neo Darwinian problem domain, and for this to be the case, two conditions must be satisfied: 1) Weismann's barrier must be porous, and 2) the proposal of a potential mechanism that allows for soma to germ-line feedback.

1. The porosity of the Weismann barrier.

The Neo Lamarckian program's hard core requires that information, at least in some cases and for some characteristics, flows from environment to hereditary material. The Weismann barrier is an assertion that heritable material only flows from germ cells to somatic cells, and never in reverse. This "barrier" prevents soma to germline feedback. While Weismann was wrong about there being a physical barrier around all germ cells, protecting them from outside influence, the implication that environmental information does not affect hereditary information finds a correlate in the Central Dogma. John Maynard Smith makes it clear what must be done if Neo Lamarckism is to be tenable: "The greatest virtue of the central dogma is that it makes clear what a Lamarckian must do—he must disprove the dogma." (p. 66.)

The Central Dogma represents a uni-directional information flow from DNA→RNA→Protein. "It is not observed, nor indeed is it conceivable, that information is ever transferred the other way around…" (Grasse, p. 221.) However, in 1970 Howard Temin announced the discovery of "Reverse Transcriptase," an enzyme that allowed RNA to transcribe its own DNA. Eventually it has been found that reverse transcriptase exists in most animal cells, common retroviruses, endogenous retroviruses, and transposable elements of DNA (Hoenigsberg, 2003). So one element of the Dogma often does not hold true—information can flow from RNA to DNA. It is conceivable that DNA could receive information about environmental needs through the action of reverse transcriptase; this is of course speculative, though Temin himself noted the possibility: "In extreme cases, one could imagine that a product of protovirus evolution would infect the germ-line, become integrated there, and thus also affect progeny organisms. Such a process could provide part of a mechanism for inheritance of some acquired characters." (H. Temin, p. iv.) Moreover, recently proposed Principle of Recursive Genome Function (Pellionisz, 2008) offers to challenge even the widespread belief that information does not pass from proteins to RNA or DNA.

The action of Reverse Transcriptase is proof of the mere possibility that the Weismann barrier is porous in terms of information passing from environment to DNA. However, DNA is not the only "hereditary material" to be carried across generations of reproducing individuals. Jablonka and Lamb identify four general types of Epigenetic Inheritance Systems (EIS's): 1) Self-Sustaining Loops, 2) Structural Inheritance, 3) Chromatin Marking, and 4) RNA Interference (RNAi). Usually, biologists associate EIS's with ontogeny and development, because EIS's help to preserve gene expression across *cellular* generations. However, EIS's can also be preserved across *organismal* generations, in most major taxa. "Epigenetic variations can be transmitted not only in cell lineages but also between generations of organisms…these variations play a significant role in adaptive evolution." (Jablonka & Lamb p. 137) More importantly, epigenetic variations are often sensitive to environmental circumstances, such as with methylation patterns on DNA. In fact, EIS's are evolutionarily valuable precisely *because* they allow the phenotype to adjust gene expression with relation to the state of the environment and the needs of the organism. That these environmental cues can be inherited across generations is another facet to the porosity of the Weismann barrier.

2. A mechanism to allow for IAC.

While EIS's may comprise a hereditary system on their own, the question remains as to whether epigenetic modifications actively alter germline DNA. However, a sound mechanistic hypothesis has finally been offered in support of the active inheritance of beneficial, somatically derived mutations.

In 1979, E.J. Steele composed a hypothesis to account for the hereditary transmission of acquired immunological characteristics in mice and idiotypy in rabbits, called the Somatic Selection Hypothesis. The hypothesis is startlingly familiar, in that it echoes Darwin's pangenesis theory, which earlier served as a bridging principle between the Darwinian program and Lamarck's adaptive force. Steele even goes so far as to quote a passage from Darwin's pangenesis theory in the opening section of his argument for the Somatic Selection Hypothesis. I have summarized the hypothesis for soma to germ-line feedback below (Steele, Somatic Selection, p. 55-56):

1) Generation of somatic mutations and their clonal selection and proliferation under favorable environmental stimuli. (Ex. rapidly reproducing liver cells being somatically selected for toxin resistance)
2) Capture of clonally packaged information by an endogenous RNA vector.
3) Somatically selected mutant gene is inserted into germline DNA through reverse transcription.
4) Darwinian selection for progeny with somatically acquired mutant gene.

The above mechanism could apply whenever there is somatic selection for a trait that improves fitness, such as specific toxin resistance among liver cells, or certain acquired immunities. It does not, however, imply such ridiculous notions as a child's inheritance of large arms from its blacksmith father or the giraffe's long legs and neck resulting from its ancestors' habit of stretching for high foliage. It should be clear that the somatic selection hypothesis, as well as EIS's, do not result in the inheritance of just any acquired character.

The two conditions for competition are satisfied in light of the above recent developments. So it is at least *possible* that the Neo Lamarckian program's problem domain be expanded to overlap with Neo Darwinism's problem domain. But is Neo Lamarckism a competitive *alternative*? The simple answer is, *no.* If we consider the Neo Lamarckian program to consist primarily of Lamarck's adaptive force resulting in adaptation, the program is simply too limited to engage with all of micro and macro evolution. For one, EIS's and Steele's hypothesis will only apply to a limited number of cases, so even with regard to localized functional adaptation, Neo Lamarckism cannot account for the full range phenomena. Weismann's barrier is porous, but not always and not everywhere. In those places where Weismann still generally applies, Neo Lamarckism cannot compete with Neo Darwinism for explanatory roles. In this way, the two programs are competitive with regard to some areas, but exclusive to others: they are not alternatives.

At this point one may object that I have construed the Neo Lamarckian program too narrowly. So let us suppose that Neo Lamarckism is composed not only of Lamarck's adaptive force, but also of the components of Neo Darwinism. The program asserts that both IAC and Natural Selection (along with genetic drift, the Baldwin effect, etc.) play a role in the micro and macro-evolution of organic life. Now, we have something eerily similar to Darwin's original research program. Natural Selection on heritable variation still operates as it did before, only now Lamarck's adaptive force is a possible explanation for adaptations under conditions where Weismann's barrier is porous or non-existent. If this version of Neo Lamarckism were set aside Neo Darwinism, we would have to conclude that Neo-Lamarckism is merely Neo-Darwinism with the additional claim that, in some conditions, IAC results in local adaptation and may contribute to speciation. This is essentially what Matsuda (1987) has offered with his proposal of "pan-environmentalism." He studied cases for which "a new evolutionary process was initiated by new environmental stimuli that have induced egg-size enlargement and consequently accelerated development" (p. 33). Pan-environmentalism expands the explanatory scheme of Neo Darwinism through incorporating the concepts of genetic assimilation and the Baldwin effect, though it does not alter Neo Darwinism's "hard core." In so doing, Matsuda, and others who would construe the Neo Lamarckian program very broadly, are not inventing an alternative to Neo Darwinism, but exploring ways of *expanding* the dominant Neo Darwinian program: its hard core remains the same, while the protective belt is adjusted to accommodate specific concepts such as genetic assimilation, EIS's, and yes, even soma to germ-line feedback. Simply naming an expanded Neo Darwinian program something else does not create a competitive alternative; these are simply attempts to refine and optimize a very general program.

When Kimura (1983) argued for the importance of the random effects of "neutral selection" on the distribution of gene frequencies, he was forwarding a program that was competitive with standard accounts of how selection adjusts allele frequencies within populations. However, it does not make sense to characterize Kimura's more specific program as a competitive alternative to Neo Darwinism—he was challenging the *relative significance* of Natural Selection versus the random effects of his neutral theory on changes in allele frequencies in certain populations. The neutral theory takes for granted and accepts the general Neo Darwinian program, but competes with other accounts of change in allele frequency at lower levels of generality. After a few decades, the mini-research program of 'Neo-Darwinism + neutral theory' is being re-integrated into mainstream Neo Darwinism. A widely construed Neo Lamarckism, of the pan-environmentalism variety, would represent the same sort of competition for Neo Darwinism as the neutral theory—a competitive alternative for other programs explaining micro-evolution in various ways, but nonetheless subsumable by the larger, more mainstream Neo Darwinian program.

The mathematical population models of the Neo Darwinian program are designed to accommodate more variables than simple Natural Selection. Drift, mutation, draft, neutral selection, heterozygote advantage, etc. all can influence the spread of alleles through populations. There is no technical barrier to preventing the simulation of the effects of IAC within the population models of Neo Darwinism (DeCastro, 2006); it is simply another variable among many. The barrier, as has been said, is Weismann's, and it has been integrated into the Neo Darwinian protective belt for far too long. Until this part of the Neo Darwinian protective belt is adjusted, there is no way for Neo Darwinism to accommodate Lamarck's adaptive force. However, as the Neo Darwinian program has begun to incorporate the newly acknowledged discipline of evolutionary development, a field that takes the role of the environment very seriously, the prospects of a less constraining Weismannian assumption replacing the more rigid version now accepted are increasing.

So a narrowly construed version of Neo Lamarckism competes with Neo Darwinism on a low level of generality and with regard to specific kinds of problems, say, speciation when certain conditions for the porosity of Weismann's barrier are assumed to be met. At their most general level, these two programs are not competitive alternatives, as Popper imagines, and some modification of Neo Darwinism's protective belt could even accommodate a role for IAC under certain conditions. A more widely construed Neo Lamarckian program, while a more complicated case, still does not offer the kind of competitive alternative that Popper suggests, because it merely represents an extension of Neo Darwinism's explanatory tools, without a modification to the hard core of the research program. Regardless of how narrowly Neo Lamarckism is defined, it never occupies the role that has been allotted to it—one side of a competitive dichotomy opposing the whole of Neo Darwinism. To make this very clear we need look no further than those who allegedly work under a Neo Lamarckian program. Steele is an experimental immunologist. He accepts the hard core of the Neo Darwinian program, but rejects the more specific assertion that Weismann's barrier prevents all IAC, and has tried to experimentally demonstrate his suspicions, to some success (Steele, 1998). Eugene Balon (2001) believes Neo Darwinism to be too gene-centric; sometimes phenotypic change precedes genotypic change, and EIS's can "jump start" speciation events. Despite this, Balon accepts the assumptions of Neo Darwinism at a general level—disagreement occurs at lower levels of generality. If one desires a competitive alternative to Neo Darwinism, they would need something more akin to Intelligent Design, which asserts a hard core that is contradictory to Neo Darwinism (I acknowledge ID is not a valid research program; my point is simply illustrative).

What is far more likely to arise, as far as competition between Neo Lamarckism and Neo Darwinism, are relative significance disputes. These are not arguments about *what* happens, or even *what cause is the correct cause* given some phenomenon, but *which cause is more significant relative to the other*. Within the research program of Neo Darwinism, there is an understanding that "evolution has resulted in a *variety* of reproductive systems, consistent with a variety of mechanisms of speciation. Faced with this variety, evolutionary biologists do not argue about which mechanism of speciation is the correct one; rather, they argue about the relative significance of each account" (Beatty, p. 346). When Darwin's program incorporated Lamarck's adaptive force in the 19th century, the competition between Lamarckian and Darwinian explanation was exactly this sort—one of relative significance. That Neo Lamarckism today can potentially explain some adaptation and speciation does not imply a threat to the roles of Neo Darwinian models, it merely implies that multiple accounts may adequately describe some area of phenomena. Biologists know this to be the case, but Neo Lamarckian mechanisms are greeted with a special type of dismissal relating to the belief that they are part of an entirely alternative system, which is simply not the case.

IV. CONCLUSION

Given that Lakatos, Popper, Laudan and Kuhn all view competition as a positive influence regarding the progress of science (Smith, 2003), the overwhelming tendency to consider the Darwinian/Lamarckian relationship to represent a competitive dichotomy is understandable. However, this tendency may have actually *delayed* scientific progress in rigidifying the endorsers of each program against claims made by the other, when the nature of their assumptions merits a more accommodating exchange of ideas. For example, "The heritability of suborganismal variation in many organisms is a necessary consequence of known developmental pattern. It is not only fact, it is one of the capital facts of biology. A significant source of genetic variation in a broad spectrum of organisms is simply not incorporated into modern evolutionary theory…the synthetic theory cannot be incorrect; it can only be incomplete" (Buss, p. 25). This "incompleteness" derives from biologists' need to describe a process, evolution, which by its very nature produces a variety of interacting mechanisms requiring a variety of explanations. "To expect a single mechanism underlying an entire domain of biological phenomena, we would have to assume that one mechanism evolved in a common ancestor of all the taxa covered by the domain, and that the mechanism has been maintained in each of those taxa ever since, and/or we would have to assume that the very same mechanism arose independently and has been maintained in all the taxa covered by the domain" (Beatty, p. 436). Evolution is not so constrained, however. It is a creative process and as such, we should allow and even *expect* that some lines of descent have developed ways of allowing for more successful adaptations via feedback from environmental pressures. The Neo Lamarckian program merely represents a particular explanation of speciation and adaptation among many others, and is amenable to a slightly modified Neo Darwinian program. The type of competition that would result from a resurgent Neo Lamarckian program would be the same that results from competition *within* the Neo Darwinian program: competition for relative significance. This kind of competition implies theoretical pluralism, not eliminative alternatives. Taken this way, the question ceases to be *could a Neo Lamarckian program replace Neo Darwinism?*, and becomes, *how significant are Neo Lamarckian mechanisms in evolution, and how are we to incorporate them into the Synthetic theory?*

In 1987, Matsuda (p. 33) investigated the role of environmental stimuli on amphibian development and evolution via genetic assimilation. In a typical response, a review claimed that “there can be little point in taking Matsuda’s thesis seriously… because it does not fit traditional evolutionary theory.” (Duncan, 1985) It is this type of reaction that I hoped to address with this project. That Lamarckian programs of the past have at times represented incompatible alternatives to Darwinian programs is certainly the case. But research programs are evolving, flexible entities, and the relationship between the two discussed here has changed dramatically over time. Neo Darwinism may soon need to modify its gene-centric, Weismannian approach in order to account for a wider array of evolved processes that may include non genetic inheritance, IAC, and genetic assimilation, among others. In so doing, “traditional evolutionary theory” may find itself evolving *around* the Neo Lamarckian program, rather than *against* it.

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