Viva Lamarck: A Brief History of the Inheritance of Acquired Characteristics

"Men who strive in their works to push back the limits of human knowledge know well that it is not enough to discover and prove a useful truth that was previously unknown, but that it is necessary also to be able to propagate it and get it recognized."[1]

A leading evolutionist recently observed that the great questions in evolutionary theory remain much the same today as they were in Darwin's time.[2] Certainly this observation applies to the debate over the inheritance of acquired characters, commonly known as Lamarckism, after Jean Lamarck, author of the first systematic theory of evolution. The debate over the reality of Lamarckian ideas has raged for the better part of a century and a half and shows no signs of abating. Indeed, as I write, the controversy has been rekindled over the announcement of new experiments allegedly supporting the possibility of inheritance of acquired characters.

In an attempt to understand the historical background and theoretical significance of this controversy we will offer here a brief outline of the history of the inheritance of acquired characters. This outline will include a summary of Lamarck's theory of evolution; an assessment of the validity of its rejection by Weismann and Neo-Darwinism; and a discussion of recent developments including the modern revival of the inheritance of acquired characters by Steele and Gorczynski.

LAMARCK AND HIS THEORY OF EVOLUTION

In a discussion of Lamarck's theory of evolution, C. H. Waddington, a distinguished contributor to the Neo-Darwinian synthesis, observed that:

> "Lamarck is the only major figure in the history of biology whose name has become, to all intents and purposes, a term of abuse. Most scientist's contributions are fated to be outgrown, but very few authors have written work which, two centuries later, is still rejected with an indignation so intense that the skeptic may suspect something akin to an uneasy conscience."[3]

The virulent nature of the debate over Lamarck's theory of evolution has made it difficult to arrive at a fair assessment of this pioneer's rightful place in biological thought. Until recently the history of Lamarckism has been written by participants in the debate; i. e., by those who generally had an axe to grind. Mayr concedes this point, offering at the same time a parting shot at Lamarck:

> "As long as the battle between Darwinism and Lamarckism was raging, it was quite impossible to undertake an unbiased evaluation of Lamarck. For this we are now ready, after

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[1]J. Lamarck, *Philosophie zoologique* (Paris, 1809), Vol. 2, p. 450. As translated by R. Burkhardt, "Lamarck and the Politics of Science," J. Hist. Biol. 3 (Fall 1970), p. 297.

[2]N. Eldredge, *Unfinished Synthesis* (New York, 1985), p. v.

[3]C. H. Waddington, *The Evolution of an Evolutionist* (London, 1975), p. 38.

> it has been demonstrated conclusively that the various causal explanations of evolution, usually designated as Lamarckism, are not valid."[4]

In the past several decades scholars have begun to reassess Lamarck's contribution to evolutionary thought and in the process great gains have been made towards separating fact from fiction as regards the development and significance of his theories. The genesis of Lamarck's ideas on evolution can be traced to the final years of the 18th century, during which time Lamarck was a participant in the vital intellectual milieu that characterized Paris at the time. Through something of an accident Lamarck had been appointed the head of the invertebrate department of the famous Museum d'Histoire Naturelle Institute in 1793, at the time the world's foremost center for biological studies. Coming on the eve of his fiftieth birthday, this appointment marked something of a departure for Lamarck, who had earlier distinguished himself as a botanist.[5]

Lamarck's evolutionary views are first detectable around 1800 and were subsequently published in systematic form in *Recherches sur l'organisation des corps vivans* (1802), *Philosophie Zoologique* (1809), and *Histoire naturelle des animaux sans vertebres* (1815-1822). Lamarckism, inasmuch as it is understood at all by the majority of biologists, connotes little more than a belief in the inheritance of acquired characters. While it is true that this belief was central to Lamarck's understanding of the evolutionary process, it is also true that it represented only one aspect of an otherwise complete theory of evolution. Indeed, for Lamarck the inheritance of acquired characters was little more than a truism, obvious to all and requiring no detailed documentation.

Lamarck recognized two principal factors behind the evolution of living forms: the first being an inherent tendency of organic matter to reach new levels of complexity; the second being the modifying capacity of the environment. These factors are apparent in the following quote from *Philosophie Zoologique*:

> "The state in which we now see all the animals is on the one hand the product of the increasing composition of 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

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[4]E. Mayr, "Lamarck Revisited,"J. Hist. Biol. 5 (1972), p. 55.

[5]In addition to botany Lamarck had dabbled in many other sciences, including geology, meteorology, chemistry and physics. Far from distracting Lamarck, these forays into other sciences provided him with several of his central insights into the nature of living forms. Lamarck's career in botany, for example, led him to emphasize the role of the environment as a modifying influence on the forms of animals. Lamarck's researches into geology, similarly, made him a strong believer in uniformitarianism, and it was as a direct result of his attempt to refute catastrophism and the possibility of widespread extinction—according to Burkhardt—that Lamarck was initially led to question the mutability of species. See R. Burkhardt, *The Spirit of System: Lamarck and Evolutionary Biology* (Cambridge, 1977), pp. 130-137. Lamarck's researches into meteorology, where he had discovered that the Moon exerted some sort of influence upon the atmosphere of the Earth—and consequently upon the fluids of living things, comparable to its effect on tides—likewise appears to have played a role in the theoretical prominence in Lamarck's writings of the formative influence of vital fluids. Lamarck's intimate acquaintance with invertebrates, such as comb jellies, where one can actually witness the vital fluids circulating about the organism, no doubt influenced him in this belief as well.

> continually tend to destroy the regularity in the gradation of the increasing composition of organization."[6]

While the former factor is well worth attention, it is Lamarck's emphasis on environmental factors which historically has received the most notoriety, and it is this factor which will occupy us in this essay.[7] According to Lamarck, the first steps towards modification of form are precipitated by changes in environmental circumstances, these changes being followed by an organism's subsequent attempt to adapt to them. A change in environmental circumstances necessitates new needs, which in turn lead to changes in an organism's behavior. These changes in behavior, once established as habitual, give rise to functionally appropriate changes in form. Lamarck's own words are as follows:

> "The environment affects the shape and organization of animals, that is to say that when the environment becomes very different, it produces in course of time corresponding modifications in the shape and organization of animals. It is true if this statement were to be taken literally, I should be convicted of an error; for whatever the environment may do, it does not work any direct modification whatever in the shape and organization of animals. But great alterations in the environments of animals lead to great alterations in their needs, and these alterations in their needs necessarily lead to others in their activities. Now if the new needs become permanent, the animals then adopt new habits which last as long as the needs that evoked them."[8]

Lamarck's theory thus places a heavy emphasis on an organism's behavior as an active agent in evolutionary development. It is an animal's habitual behavior which ultimately determines its form, with form following function in Lamarck's understanding. Such a view represented a significant departure from the standard view at the time, which supposed that an animal's divinely ordained form predetermined its mode of life and behavior.[9]

Lamarck summarized his view of evolution in two laws:

> "(1) The production of a new organ in an animal body results from a new need which continues to make itself felt, and from a new movement that this need brings about and maintains; (2) All that nature has caused to gain or lose by the circumstances to which their race has been exposed for a long time, and, consequently by the influence of a predominant use or constant disuse of an organ or part, is conserved through generation in the new

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[6] Lamarck, *op cit.,* Vol. I, p. 145.

[7] Lamarck's belief in an inherent tendency towards complexity has given rise to numerous interpretations, and Lamarck's statements on this factor are by no means unambiguous. Corsi, most recently, has stated that: "In the texts of 1809 and 1815, the 'tendency to complication' and the 'power of life', far from implying an intrinsic finality in life and its properties, simply indicated the 'fact' that organic structures grew more complex." See P. Corsi, *The Age of Lamarck* (Berkeley, 1988), p. 193. Here it is interesting to note that similar ideas have been expressed by other distinguished scientists. Peter Medawar, for example, recently lamented that: "The main weakness of modern evolutionary theory is its lack of a fully worked out theory of variation, that is, of candidature for evolution, of the form in which genetic variants are proffered for selection. We have therefore no convincing account of evolutionary progress—of the otherwise inexplicable tendency of organisms to adopt ever more complicated solutions of the problems of remaining alive." Quoted in R. Dawkins, *The Extended Phenotype* (San Francisco, 1982), p. 165.

[8] Lamarck, *Philosophie zoologique* (London, 1914), Vol. I, pp. 107-108.

[9] See Corsi, *op cit*., p. 100.

individuals descending from them, provided that these acquired changes are common to the two sexes or to those which have produced these new individuals."[10]

Lamarck attempted to provide illustrations of how environmental circumstances had influenced the form of animals but here it must be said that his arguments were not especially persuasive, especially when it came to explaining the acquisition of new organs. One positive example of modification of form provided by Lamarck is worth mentioning as it has long since been regarded as a classic example of the inheritance of acquired characters by Darwin and many other naturalists: namely, the modification in the location of the flatfish's eyes.[11] Here the flatfishes' habit of swimming on one side has resulted in its eyes "migrating" to the upper side of its head.

Lamarck was more convincing when discussing the modifying effects of disuse upon form. As an example of this type of organic change Lamarck cited the absence of teeth in most whales, due, apparently, to their propensity for feeding upon filtered plankton which rendered teeth unnecessary. This feature contrasted sharply with the well-developed teeth of related mammals, and indeed whales possess rudimentary teeth as embryos. The rudimentary nature of the whale's teeth remains valid today as evidence of organic evolution.[12]

It should be noted in passing that Lamarck recognized the existence of other factors whereby living forms might become modified, including the direct effects of the environment (confined primarily to plants and lower animals), effects due to accidental variation (such as sports), hybridization, and domestication.[13] Many of these factors would reappear in Darwin's theory of evolution a half century later.

Lamarck's observations on accidental agents of change emphasize the fundamental difference between his conception of evolution and that of modern biology and offer a suitable jumping off point from which to begin our analysis. Lamarck insisted that accidental causes of variation were subordinate in importance to those derived from force of habit:

> "One must distinguish between varieties obtained accidentally during the development of an embryo, either in a grain, an egg, or a uterus, from those which are formed during the course of the life of the individual; the variety resulting from the first cause being less conservable than that from the second."[14]

It is the emphasis on the accidental nature of variation, of course, which distinguishes Darwin's theory of evolution from that of his great predecessor, and it is this element, together with the concept of natural selection, which survives in the modern view of the evolutionary process, commonly termed the Neo-Darwinian synthesis.[15] Indeed the

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[10]Burkhardt, *op cit*., p. 166.

[11]Lamarck, *op cit*., Vol. I, p. 252.

[12]The same argument applies to the whale's rudimentary hind-legs.

[13]Burkhardt, *op cit*., pp. 179-181.

[14]Burkhardt, *op cit*, p. 179.

[15]It should be noted, however, that by accidental variation Darwin meant phenotypic variation while modern biologists mean genotypic variation.

modern view represents a total inversion of Lamarck's system in that it holds that only accidental changes are conservable—these changes being conceived as arising in the genome alone—with those changes arising during the life of the individual having no conservability whatsoever.

CUVIER, DARWIN, AND THE RECEPTION OF LAMARCK'S THEORY OF EVOLUTION

It is well-known that Lamarck's theory of evolution did not gain favor with his contemporaries. Here Burkhardt has noted that: "with the exception of a few brief and scattered comments Lamarck's evolutionary ideas were publicly received in silence."[16] Geoffroy St. Hilaire, himself an early proponent of evolutionary views, offered the following portrait of Lamarck's final years: "attacked on all sides, insulted even by odious jests, Lamarck, too indignant to respond to such cutting epigrams, submitted to the insult from them with a sorrowful patience."[17]

Indeed, for all practical purposes, Lamarck's theory was ignored until Darwin's *Origin of Species* made evolution a household word. At that time various writers began to call attention to Lamarck's pioneering role in evolutionary thought, foremost among these being Samuel Butler and Ernst Haeckel.[18]

Why, it is necessary to ask, were Lamarck's views so offensive to the ears of his contemporaries? Here we can only offer a few general observations as a full answer to this question would require volumes. That Lamarck expressed evolutionary views in a time generally characterized by creationist views certainly did not bode well for their acceptance. Yet this is not likely to be the sole explanation of Lamarck's fate as other French naturalists also expressed themselves on the possibility of organic mutability without being heaped with the abuse that afflicted Lamarck.

In attempting to account for the failure of Lamarck's theory of evolution Burkhardt calls attention to the empirical nature of French science at the time of Lamarck and cites the frailty of Lamarck's evidence:

> "It is often said that Lamarck's evolutionary theory was rejected in its own day simply because people at the beginning of the nineteenth century were unaccustomed to thinking in evolutionary terms. Lamarck, in other words, was too far ahead of his time to be appreciated. What seems to be more nearly the truth, at least with respect to the French scientific community, is that Lamarck's theory of evolution was rejected not because the idea of organic mutability was virtually unthinkable at the time, but because Lamarck's support of that idea was unconvincing and because, more generally, the kind of speculative venture Lamarck had embarked upon did not correspond with contemporary views of the kind of work a naturalist should be doing…His arguments for evolution took the form of broad

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[16]R. Burkhardt, "Lamarck and the Politics of Science," J. Hist. Biol. 3 (Fall 1970), p. 291.

[17]Burkhardt, *op cit*., p. 293.

[18]S. Butler, *Evolution, Old and New* (London, 1921).

> assertions accompanied by a limited number of examples but no solid empirical foundation."[19]

Lamarck's manner of presenting his evolutionary hypotheses must bear some of the responsibility for the fate of his ideas. A cumbersome and disjointed style of writing, a penchant for speculation and offering grandiose interpretations of the various natural sciences, a reliance upon outmoded understandings of chemistry and physics, all conspired to render Lamarck's views unpalatable to the majority of his scientific peers.[20] Here again, however, it is well-known that other pioneers in science have had cumbersome styles, a perfect example being Darwin himself, and thus style and presentation alone cannot account for the rejection of Lamarck's ideas.

An important factor in the dismissal of Lamarck's theory was the shabby treatment it received at the hands of Georges Cuvier, the justly renowned pioneer of paleontology and comparative anatomy. The story of Cuvier's ridiculing caricature of Lamarck's theory, delivered as a eulogy, has been chronicled many times.[21] Suffice it to observe here that Cuvier's attack upon Lamarck's views, coming from the most distinguished French zoologist of the time, carried a lot of weight and temporarily banished Lamarck's ideas from serious consideration. It is possible to trace several of the misconceptions which have dogged Lamarck's theory directly to Cuvier's eulogy, foremost among these being the claim that Lamarck's theory envisaged animals wishing themselves new organs.[22] The ludicrous example of the giraffe wishing itself a longer neck continues to be repeated to this day.

It is notable that the same misconception appears in several of Darwin's references to Lamarck, an indication, perhaps, of the widespread influence of Cuvier's critique.[23] In a letter to J. D. Hooker, for example, Darwin begs: "Heaven forfend me from Lamarck[s] nonsense of…'adaptations from the slow willing of animals'."[24] An additional factor in

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[19]Burkhardt, *The Spirit of System*, *op cit*., pp. 201-202, 210.

[20]Corsi offered the following observation on Lamarck's style and its influence upon the fate of his theories: "The conceptual and stylistic difficulties characteristic of Lamarck's works made it difficult to read his transformist texts with accuracy. The story of the fate of his ideas—and of the hypotheses variously inspired by his theories—immediately became a tale of partial readings, of biased emphases on different points of his thought." P. Corsi, *The Age of Lamarck* (Berkeley, 1988), p. 206.

[21]See the extensive discussion in H. Cannon, *Lamarck and Modern Genetics* (Springfield, 1959), pp. 8-31. See now also T. Appel, *The Cuvier-Geoffroy Debate* (New York, 1987), pp. 168-169. On the general reception of Lamarck's ideas Burkhardt notes that: "A scientist and his work may be discredited by means of innuendo rather than through open confrontation. Such mechanisms seem to have been operating in respect to Lamarck's evolutionary ideas." R. Burkhardt, "Lamarck and the Politics of Science," *Journal of the History of Biology* (Fall, 1970) Vol. 3:2, p. 284.

[22]A. Packard, *Lamarck* (New York, 1980). That the same misconception continues to this day is evidenced by the statement of Gruber, a biographer of Darwin, that Lamarck "believed that 'will' was an essential part of all adaptive processes." *Early Writings of Charles Darwin* (Chicago, 1980), p. 47. Nothing could be further from the truth as Burkhardt and many other commentators have demonstrated.

[23]Cannon notes that the eulogy of Cuvier was published in the *Edinburgh New Philosophical Journal* in 1836, the year of the return of the Beagle, and observes of Darwin's references to Lamarck: "his criticisms all appear to be based on the eulogy." *op cit*., p. 26.

[24]F. Darwin, ed. *More Letters of Charles Darwin* (New York, 1903), Vol. I, p. 41.

Darwin's misunderstanding of Lamarck's views—and one which played an indeterminable but probably significant role in their poor reception outside of France—was the lack of a suitable translation of Lamarck's writings.[25] Lamarck's *Philosophie Zoologique*, for example, was first translated into English in 1914.[26]

Cuvierian propaganda and the language barrier aside, it is nevertheless a fact that in his published writings and letters Darwin typically referred to Lamarck and his theory in a derogatory manner, denying any Lamarckian influence upon his work.[27] In a letter to Lyell, for example, Darwin refers to Lamarck's *Philosophie zoologique* as "a wretched book, and one from which (I well remember my surprise) I gained nothing."[28] Darwin repeated this claim in another letter: "I got not a fact or idea from it."[29]

Such statements, however, are demonstrably untrue. That Lamarck's writings had a profound influence upon the development of Darwin's views on evolution is obvious upon review of the formative period of Darwin's ideas.[30] It is known that Darwin encountered Lamarck's theories while at Edinburgh (1825-1827) where he read parts of Lamarck's *Systeme des animaux sans vertebres*, in which Lamarck's evolutionary views were clearly expressed.[31] This was well before the famous voyage of the Beagle (1831-1836), and long before Darwin had any personal inclination towards accepting the evolutionary hypothesis. (Indeed historians have concluded that it was not until at least 1837 that Darwin came to abandon his belief in the fixity of species).[32]

Darwin's personal notebooks compiled during the period in which he came to accept the reality of evolution (1837-1840), some twenty years before the publication of *Origin of Species*, likewise attest to the decisive influence of Lamarck. There Darwin referred to Lamarck and his theory in the most glowing of terms:

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[25]D. Kohn suggests that Darwin may have been misled here by Lyell's translation of Lamarck's besoin "needs" as "wants" (Lyell's *Principles of Geology* had contained a lengthy summary of Lamarck's theory of evolution). See Kohn's discussion of this problem in "Theories to Work By: Rejected Theories, Reproduction, and Darwin's Path to Natural Selection," in *Studies in History of Biology* (Baltimore, 1980), Vol. 4, ed. by W. Coleman & C. Limoges, p. 167.

[26]Mayr, *op cit*., p. 56.

[27]Thus Grinnell observes that: "This is the pattern in all Darwin's publications; Lamarck is either condemned or ignored." G. Grinnell, "The Rise and Fall of Darwin's Second Theory," J. Hist. Biol. 18: 1 (Spring 1985), p. 52.

[28]F. Darwin, ed. *The Life and Letters of Charles Darwin* (New York, 1887), Vol. II, p. 199.

[29]Mayr, *op cit*., p. 90.

[30]Corsi has observed that while Lamarck's views were rarely faithfully represented they nevertheless exerted a decisive influence upon the scientific community in the years after his death: "There is no doubt that in early and mid-nineteenth century Europe the debate on Lamarck—however interpreted—constituted a key factor in the formation of the broad pro-evolutionary culture that greatly influenced, and often misdirected, the reception of Charles Darwin's *Origin of Species*." See P. Corsi, *The Age of Lamarck* (Berkeley, 1988), p. 268.

[31]F. Egerton, "Darwin's Early Reading of Lamarck," in *Isis*, pp. 454-455. Exactly when Darwin first learned of Lamarck's theory of evolution is still something of a mystery.

[32]Gruber suggests 1837 marked the year of Darwin's conversion. See *Early Writings of Charles Darwin* (Chicago, 1980), p. xvii. Kohn concurs with this judgement. See D. Kohn, *op cit*., p. 67.

"Lamarck was the Hutton of Geology, he had few clear facts, but so bold and many such profound judgment that he foreseeing consequence was endowed with what may be called the prophetic spirit in science. The highest endowment of lofty genius."[33]

Prominent also in these notebooks is the belief that habit determines structure, one of the most distinctive features of Lamarck's theory of evolution. Thus Darwin proclaimed: "According to my views, habits give structure, habits precede structure, habitual instincts precede structure."[34] The same idea is expressed in another passage: "All structures either direct effect of habit, or hereditary and combined effect of habit."[35] Kohn, in a lengthy analysis of Darwin's conversion to the evolutionist position, notes that Darwin's formative ideas on the subject were usually, if not always, borrowed and that the "Darwinism of 1837 was not far removed from the Lamarckism of 1809."[36]

Such evidence casts a new light on Darwin's derogatory remarks towards Lamarck in his published works and letters. Indeed, there is much reason for believing that Samuel Butler was right all along in maintaining that Darwin's concern for priority with regard to the development of the theory of evolution led him to conceal his great debt to the French pioneer.[37]

As the foregoing intrigue reveals, the relationship between the Lamarckian and Darwinian theories of evolution is far more complex than generally acknowledged. College textbooks typically ignore Darwin's indebtedness to Lamarck and represent the relationship between the theories of Lamarck and Darwin as one of clearcut progress, with Darwinism triumphing over the discarded Lamarckism. Such an interpretation glosses over the fact that Darwin himself was a Lamarckian—inasmuch as this term connotes a belief in the inheritance of acquired characters. This was hardly an incidental aspect of Darwin's thought, as is sometimes suggested; rather a belief in the inheritance of acquired characters was integral to Darwin's understanding of the evolutionary process.[38] Indeed, from his first notes on evolution to his final thoughts on the matter Darwin maintained that Lamarckian inheritance was essential in explaining many of the most difficult questions surrounding the evolution of living organisms, including the inordinate growth of the human brain, the loss of structures through disuse, the origin of

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[33]Grinnell, *op cit*., p. 53.

[34]*Ibid*., p. 63.

[35]*Ibid*., p. 69.

[36]See Kohn, *op cit*., pp. 72, 98, 131.

[37]S. Butler, *Evolution, Old and New* (London, 1879); *Unconscious Memory* (London, 1880), p. 39; *Luck and Cunning* (London, 1887), pp. 177-178. In 1890 Butler was led to quip of Darwin: "These facts convince me that he was at no time a thoroughgoing Darwinian, but was throughout an unconscious Lamarckian, though ever anxious to conceal the fact alike from himself and from his readers." See "Deadlock in Darwinism," in *Collected Essays* (London, 1925), Vol. II., p. 14.

[38]See Mayr's discussion of this aspect of Darwin's thought in the preface to C. Darwin, *Origin of Species* (Cambridge, 1964), pp. xxiv-xxvii. See also E. Cochrane, *Psychology, Psychologists, and Evolution* (Ames, 1982), pp. 22-30.

many instincts, etc.[39] Darwin reaffirmed his "Lamarckism" in the preface to *The Descent of Man,* where he complains that his critics have overlooked this element in his writing. There Darwin reiterated that he has always held "that great weight must be attributed to the inherited effects of use and disuse, with respect both to the body and mind."[40]

It is well-known that Darwin attempted to provide a physiological foundation for the inheritance of acquired characters via his theory of heredity known as pangenesis, which envisaged that gemmules (a conceptual forerunner of the gene) from the body migrated to the sex cells to inform them of changes in the body.[41] Darwin's "provisional" hypothesis represented the first comprehensive attempt to account for the phenomena of heredity by a common principle, and exerted a decisive influence upon the later theories of Galton, Weismann, and de Vries.[42]

THE RISE AND FALL OF LAMARCKISM

Thanks in part to the patronage of Darwin, but due mainly to the immense influence of the evolutionary writings of Herbert Spencer, Ernst Haeckel, Samuel Butler and others, the doctrine of the inheritance of acquired characters enjoyed what may be called a golden age during the period between 1860 and 1910. This period saw the development of the American school of paleontology associated with such influential figures as Cope, Osborn, Packard and Hyatt.[43] As Bowler points out, this American school—deemed Neo-Lamarckian by Packard because of its heavy reliance upon the inheritance of acquired characters as an explanatory agent in the modification of organic forms—was as close as the Lamarckians ever came to offering an organized community.

Paleontologists were not the only scientists to embrace Lamarckism, as Burkhardt notes:

> "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

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[39]In the *Origin of Species*, for example, Darwin observes: "I think there can be little doubt that use in our domestic animals strengthens and enlarges certain parts, and disuse diminishes them; and that such modifications are inherited." *Ibid*., p. 134.

[40]C. Darwin, *The Descent of Man* (London, 1874), pp. iii-iv.

[41]C. Darwin, *The Variation of Animals and Plants under Domestication* (London, 1868).

[42]Mayr, *op cit*., pp. 693-694.

[43]For a summary of the views of this school see P. Bowler, *The Eclipse of Darwinism* (Baltimore, 1983), pp. 118-140. See also the discussion in S. Gould, *Ontogeny and Phylogeny* (Cambridge, 1977), pp. 85-100.

> degeneration of useless organs, correlated variation, and the origin of various kinds of instinctive behavior."[44]

About 1910, however, together with the continued development of a science of genetics steeped in Mendelism and the theoretical researches of Weismann, there began a discernable tendency to question the theoretical necessity—if not the reality—of the inheritance of acquired characters. The rise of Weismann's influence was particularly apparent and was cited by numerous biologists of the period as a primary factor in the demise of Lamarckian beliefs. L. Doncaster, reviewing the situation at the turn of the century, attests to Weismann's decisive role in this controversy: "Since the publication of Weismann's theory of heredity with the great body of evidence which has been collected on the other side, opinion has turned increasingly towards the belief that acquired variations are not transmitted."[45] Mayr observes that by 1940 Weismannism had gained nearly universal acceptance.[46]

By 1930 and the development of the population genetic programs of Fisher and Wright a new era was apparent, one which emphasized experimental procedures and quantification of the results through mathematics. This school generally looked down upon the sort of indirect evidence drawn from the study of fossils and the behavior of animals which had always provided the foundation of a belief in the inheritance of acquired characters. It should be pointed out, however, that there was in fact a good deal of experimental investigation of Lamarckian inheritance. A glance at the literature of the period reveals literally dozens of experiments in which positive evidence of the inheritance of acquired characters was reported.[47] As Neo-Darwinism came to dominate biology during the thirties and forties, however, alternative explanations were offered for the experimental results suggesting a Lamarckian interpretation, and the Lamarckian hypothesis became increasingly ignored as a factor in evolutionary development. Perhaps Burkhardt was right that Lamarckism began to wane not so much from disproof, but from the death of its leading proponents and the general belief that Lamarckian inheritance was unnecessary to explain the processes of evolution: "Lamarckism was not falsified by experiment so much as it was rejected as an unnecessary hypothesis."[48]

Bowler has offered a similar assessment of the banishment of Lamarckism from the modern synthesis, adding that the failure of Lamarckian theorists to come up with a viable theory of heredity spelled their doom:

> "By the time the war threw European science into a turmoil, biologists had already begun to move away from Lamarckism. Yet the theory was never abandoned completely: 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."[49]

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[44]R. Burkhardt, "Lamarckism in Britain and the United States," in *The Evolutionary Synthesis* (Cambridge, 1980), ed. by E. Mayr and W. Provine, p. 346.

[45]L. Doncaster, *Heredity in the Light of Recent Research* (Cambridge, 1911), p. 20.

[46]Mayr, *The Growth of Biological Thought, op cit*., p. 701.

[47]P. Fothergill, *Historical Aspects of Organic Evolution* (New York, 1953), pp. 253-274.

[48]R. Burchardt, *op cit*., p. 347.

[49]Bowler, *op cit*., p. 76.

SOME ISOLATED VOICES

During the period that witnessed the ultimate eclipse of Lamarckian influence within biology several researchers stood out for their continued defense of Lamarckian ideas. Noteworthy here are Paul Kammerer, the tragic biologist whose incredible ability to breed amphibians and reptiles led to a series of notorious experiments during which many intriguing results were obtained suggestive of a Lamarckian interpretation[50]; Hans Spemann, the Nobel-prize winning embryologist whose ingenious experiments uncovered the organizer[51]; E. S. Russell, a biologist whose *Form and Function* is still regarded as a classic contribution to the philosophy of biology[52]; and F. W. Jones, a comparative anatomist whose many books provide a wealth of evidence in favor of Lamarckian inheritance.[53]

It is also noteworthy that several of the greatest figures in the history of psychology—many of whom were active during this period—also expressed a belief in Lamarckian inheritance, including Freud, Jung, Watson, McDougall, Bleuler, Pavlov and Piaget.[54] The writings of these men kept Lamarckism alive long after it had been rejected by the majority of biologists.

Why, it may be asked, did these distinguished researchers continue to adhere to a supposedly discredited form of inheritance? Their reasons were numerous and can only be briefly alluded to here. Among naturalists and psychologists alike there was a common belief that it was impossible to explain the remarkable instincts of animals without some direct transmission of the effects of experience. Freud summed up this view very succinctly:

> "If the so-called instincts of animals—which from the very beginning allow them to behave in their new conditions of living as if they were old and long established ones—if this instinctual life of animals permits of any explanation at all, it can only be this: that they carry over into their new existence the experience of their kind; that is to say, that they have

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[50]P. Kammerer, *The Inheritance of Acquired Characters* (New York, 1924). It was Kammerer's suicide in 1926, coming in the wake of the finding that one of his prized specimens had been tampered with, that effectively sealed the doom for Lamarckism in the eyes of many mainstream biologists. For a poignant, albeit partisan, account of Kammerer's experiments and their role in the Lamarckian controversy see A. Koestler, *The Case of the Midwife Toad* (London, 1971).

[51]On Spemann see R. Rinard, "Neo-Lamarckism and Technique: Hans Spemann and the Development of Experimental Embryology," J. Hist. Biol. 21: 1 (Spring 1988); also V. Hamburger, *The Heritage of Experimental Embryology: Hans Spemann and the Organizer* (New York, 1988).

[52]E. S. Russell, *Form and Function* (London, 1916); *The Interpretation of Development and Heredity* (Oxford, 1930); *The Diversity of Animals* (Leiden, 1962).

[53]F. W. Jones, *The Trends of Life* (London, 1953); *Design and Purpose* (London, 1941); *Habit and Heritage* (London, 1944).

[54]E. Cochrane, *Psychology, Psychologists, and Evolution* (Ames, 1982), pp. 160-234. It was McDougall, in fact, who published one of the final experiments attempting to demonstrate the inheritance of acquired characters. Of McDougall's research the historian Fothergill observed that it provided "one of the most elaborate biological experiments yet devised", adding that the papers describing the results "are surely models of their kind and must rank among the classics of scientific literature." P. Fothergill, *Historical Aspects of Organic Evolution* (New York, 1953), pp. 261-262.

> preserved in their minds memories of what their ancestors experienced. In the human animal things should not be fundamentally different."[55]

Lamarckism appealed especially to those researchers who held that mind and psychical factors had a role to play in evolution. While Lamarck himself had downplayed the importance of consciousness or intelligence in all but the highest life forms, other prominent Lamarckians such as Butler and Russell observed that it was Lamarck's theory which first emphasized the importance of an animal's behavior in directing its evolution, and that it was but a small step from here towards assigning psychical factors a significant influence in the mutability of organic forms.[56]

The evidence for Lamarckism, as noted earlier, was largely circumstantial in nature. A favorite ploy among Lamarckian writers was to cite the intimate adaptation of an animal's form to its environment and lifestyle, this agreement of form and function seemingly requiring some sort of direct feedback from the animal's body to its genome. As an example of this type of argument consider the striking adaptation provided by the skeletal structure of the seal.

Most mammals, upon taking to the water on a temporary basis, swim by arching their necks and throwing back their heads thereby aligning the nostrils, eyes, and ears above the water level. To attain this position it is necessary that the cervical region of the spine become bent backwards producing a convex curve of the animal's cervical column on its ventral side. Dogs customarily assume this posture whenever they take to water; seals assume it on a permanent basis. Upon noting the overwhelming probability that seals descended from terrestrial mammals, Jones offers the following analysis of their peculiar skeletal structure:

> "It is natural to assume that, at the very outset of their departure from normal terrestrial life, the ancestors of the seals produced the characteristic curvature of the cervical region only when actively engaged in swimming. It is a further justifiable assumption that, as aquatic life became more habitual, this peculiarity became increasingly impressed on the disposition of the cervical vertebrae. In the end, it became a definite and permanent feature of the adult."[57]

Jones points out that the convex form of the seal's cervical region is present in the embryo and that its hereditary nature is incontestable. This feature of the seal's anatomy, moreover, stands in striking contrast to the cervical regions of most mammalian embryos, which are curved in the opposite direction (see diagram one).

It is difficult to find fault with Jones' thesis that the seal's skeletal structure is a direct result of its aquatic lifestyle and is to be attributed to an inheritance of acquired characters. This explanation is perfectly logical and makes intuitive sense. What is the alternative? That an accidental change in the genome of the seal's terrestrial forebears caused them to acquire a uniquely curved neck, and that this newly acquired feature preadapted them for aquatic life and favored them in the struggle for survival? Or, granting that the seal's aquatic lifestyle preceded any genetic changes, is it likely that a

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[55]Freud, *Moses and Monotheism* (New York, 1939), pp. 128-129.

[56]E. S. Russell, *The Diversity of Animals* (Leiden, 1962), pp. 127-128.

[57]Jones, *Trends of Life*, p. 142.

fortuitous genetic mutation(s) occurred which established the curvature in the cervical region as a permanent feature of the species?[58]

The example of the seal's cervical vertebrae offers a vivid illustration of the explanatory power of the Lamarckian theory of evolution. This explanatory power, moreover, is acknowledged by most of the participants in the debate.[59] The sole difficulty with the theory is in coming up with a viable bio-chemical explanation of Lamarckian inheritance (more of which later). The explanatory power of the Neo-Darwinian theory, in contrast—given the rare occasion in which proponents of this position condescend to discuss specific examples of organic modification of form—stretches the credulity of the reader at every step. Mutations and selection are admittedly real phenomena; the question is can the evolution of perfectly coordinated and apparently purposeful structures be explained by the gradual accumulation of accidental changes in genetic structure, particularly when these accidental changes are envisaged as occurring at random with respect to the needs of the evolving organism?

The fact is that given any useful character it is always possible to postulate a Darwinian explanation provided that one accepts the potential adaptability of accidentally wrought changes in the genome. It is a different matter, however, if the character in question happens not to have an adaptive value. Such non-utilitarian or neutral characters have long troubled Darwinians since in such cases there can be no question of selection favoring them inasmuch as they would have no influence on survival rate or reproductive success.[60] As an example of such non-utilitarian characters we might consider the case of the tibular facets provided by certain aborigines.

Early anthropologists called attention to the strange fact that natives of Oriental descent customarily assumed a particular posture when squatting. The Oriental's mode of squatting may be contrasted with that typically assumed by Australian aborigines (see diagram two). These respective modes of squatting, it turns out, result in definite structural modifications of the tibia and related structures and are heritable in the respective peoples. Jones' discussion of these modifications, offered from the vantage point of a comparative anatomist, is worth quoting at length:

> "That the well-known squatting facets on the lower anterior border of the tibia and the upper anterior aspect of the astragulus are caused by the extreme position of dorsi-flexion of the ankle joint, maintained during the action of sitting hunkered on the heels with the buttocks raised sheer of the ground, is beyond the possibility of any dispute. No clearer case of the intimate linking of cause and effect could be found anywhere in nature. These peculiar articular facets are not developed in people who do not adopt this position of rest, nor are

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[58]This is the theory of organic selection made famous by Baldwin and the Neo-Lamarckian Osborn, later adopted and christened genetic assimilation by Waddington.

[59]Even Weismann conceded this point: "I have always emphasized the fact that it is easier to explain the transformation of species on Lamarck's principle." A. Weismann, *The Germ-Plasm* (New York, 1902), p. 408. See also Mayr, *The Growth of Biological Thought*, p. 527.

[60]It was in part because of these non-utilitarian or injurious characters that Darwin was led to develop his theory of sexual selection. See Cochrane, *op cit.*, p. 174. See also Bowler, *op cit.*, p. 216.

> they found in the embryo, foetus or new-born of such people…The squatting facets on tibia and astragalus are present in all Asiatic peoples who adopt the hunkered position of rest, but they are absent in all people who know the habitual use of chairs or of some other contrivance upon which to sit. Moreover, among those peoples who do not know the use of chairs there are various elected postures in squatting. It is well known that the Australian aborigine squats in his own peculiar, and for us very uncomfortable, position. He does not, as a habit, sit on his heels with his buttocks raised clear of the ground, like an Asiatic; but he flexes his lower limbs completely, turns the soles of his feet inwards and backwards and rests his buttocks upon the lower part of his shanks and his inturned feet. In conformity with this peculiar posture, maintained for long intervals and adopted by all individuals, he has developed perfectly definite facets on the bones of his legs and these are obviously the outcome of his posture and are entirely different from those of the typical Asiatic squatter…Now these things have been known for many years (Havelock Charles published his classical paper as long ago as 1893): they are perfectly well authenticated facts about which there can be no possible dispute. It is quite impossible to ignore them. What is the alternative to regarding them as being good evidence of the inheritance of acquired characters?"[61]

What indeed!

WEISMANN AND THE RISE OF NEO-DARWINISM

The death-knell of Lamarckism, as we have seen, is commonly traced to Weismann's theory of heredity. In 1959 the historian Conway Zirkle could look back upon the developments in biology since the appearance of Weismann's theory and offer the following assessment of his lifelong struggle against Lamarckism: "The fact that he succeeded in the fight insures him a permanent place in the history of science."[62]

Since it is Weismann's theory of heredity which is generally credited with discrediting Lamarckian ideas, a detailed analysis of Weismann's theory must form a prerequisite to any discussion of Lamarckism. Such an analysis will serve two purposes: (1) it will allow us to evaluate the theoretical basis upon which the inheritance of acquired characters first became subject to question; and (2) it will serve as an introduction for understanding the modern denial of Lamarckism inasmuch as several of the fundamental assumptions of Weismann's theory of heredity persist in the modern theory of heredity.

August Weismann (1834-1914) was truly one of the most influential thinkers in the history of biological study. During the course of a long and productive career Weismann was led to investigate most of the fundamental issues in biology, from the means of evolutionary change, to the mechanisms of heredity and development, to the biological significance of death. Throughout his career Weismann's work was characterized by the logical presentation of bold and sweeping hypotheses.

It was in an essay entitled "On Heredity," delivered as a lecture at Freiburg in 1883, that Weismann first announced his intention to hold up to question the reality of the

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[61]Jones, *Habit and Heritage*, pp. 49-50.

[62]C. Zirkle, *Evolution, Marxian Biology, and the Social Scene* (Philadelphia, 1959), p. 118.

inheritance of acquired characters.[63] Weismann offered two principal forms of argument against the Lamarckian theory, which he repeated and refined throughout his long career: (1) that the explanatory power of natural selection rendered a belief in the inheritance of acquired characters superfluous; and (2) that the facts of heredity rendered a belief in the inheritance of acquired characters impossible from a theoretical standpoint (see the following section). Weismann thus became the first prominent biologist (along with Alfred Wallace, the generally forgotten co-discoverer of the theory of natural selection) to reject the necessity of invoking the inheritance of acquired characters to explain evolution. Weismann coined the phrase the "all-sufficiency of natural selection" to describe the resulting viewpoint, and historians frequently trace the inception of Neo-Darwinism to Weismann's formulations.[64]

Weismann attempted to defend this position by demonstrating how natural selection could account for the various biological phenomena which had led Darwin and other naturalists to maintain a belief in the inheritance of acquired characters. The loss or degeneration of organs through disuse—such as short-sightedness in humans and degeneration in the eyes of cave-dwelling animals—was singled out by Weismann for analysis. (Here Darwin had written: "As it is difficult to imagine that eyes, though useless, could be in any way injurious to animals living in darkness, I attribute this loss wholly to disuse)."[65]

Here Weismann invoked his principle of panmixia—or the suspension of natural selection—and suggested that in the absence of selection accidental variations in the germ cells might accumulate which would result in a degeneration of the eyes. Weismann concluded:

> "The greater number of those variations which are usually attributed to the direct influence of external conditions of life, are to be ascribed to panmixia. For example, the great variability of most domesticated animals essentially depends on this principle."[66]

Once rendered useless an organ would become a detriment to the species insofar as it required nutrition which might be better employed elsewhere, at which point natural selection would intervene to account for the character's ultimate disappearance:

> "The complete disappearance of a rudimentary organ can only take place by the operation of natural selection; this principle will lead to its elimination, inasmuch as the disappearing structure takes the place and nutriment of other useful and important organs."[67]

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[63]This essay can be found in A. Weismann, *Essays Upon Heredity* (Oxford, 1891).

[64]E. Mayr, *The Growth of Biological Thought* (Cambridge, 1982), p. 698. It could be argued, in fact, that the modern theory of evolution is closer to the original formulations of Weismann than to those of Darwin. John Maynard Smith, a leading spokesman for the Neo-Darwinian position, acknowledges this point: "Neo-Darwinism is essentially Weismannist; that is, it holds that heritable variation is in origin non-adaptive, and that adaptive changes which occur during the lifetime of individuals (for example, acclimatisation to high altitudes) do not alter the nature of the offspring they produce. In contrast, Darwin accepted a Lamarckian view of heredity; he thought that the 'effects of use and disuse' could influence the nature of offspring, and even developed his theory of pangenesis to account for such effects…If Weismann was right, then natural selection plays an even more fundamental role than Darwin thought; it becomes the only process leading to genetic adaptation." J. Smith, *Evolution Now* (Oxford, 1982), p. 91.

[65]Darwin, *op cit.*, p. 137.

[66]*Ibid.*, p. 91.

Weismann not only sought to discredit the favorite arguments of the Lamarckians, he attempted to show that a Lamarckian interpretation was precluded in numerous examples of organic evolution. Given such phenomena as the evolution of the caste system in social insects, where the colony is divided up amongst specialized workers, soldiers, and nurses, Weismann asked how could the Lamarckian principle of the inheritance of acquired characters account for such castes when the sterile insects themselves produced no offspring?[68] If the Lamarckian principle was of no use in explaining these examples of modification of form why was it necessary elsewhere? The only alternative, according to Weismann, was to attribute the evolution of these adaptations to natural selection.[69]

Weismann's arguments presented a formidable challenge to the Lamarckian position, and indeed one can find the same arguments repeated today by leaders of the modern synthesis. Soon after Weismann published his critique, Herbert Spencer, the great English philosopher, came to the defense of the Lamarckian position. Spencer offered detailed responses to each of Weismann's arguments, his discussion of the caste system in sterile insects being especially conclusive.[70] Spencer argued that the various castes in insect colonies—far from being incompatible with the Lamarckian theory—were in fact caused by environmental factors, such as differential feeding, and that Weismann's assumption of a genetic basis of the castes was not supported by the facts.[71]

The debate between Weismann and Spencer was waged in the leading scientific journals of the day and continued until the latter's death in 1903. Suffice it to observe here that while few issues were resolved by the debate, the logical powers displayed by the respective combatants mark it as the intellectual pinnacle of the Lamarckian controversy.

WEISMANN'S THEORY OF THE GERM PLASM

It was in "On Heredity,"significantly, that Weismann first outlined his hypothesis of the continuity of the germ plasm. Inspired originally, it seems, by the observation that the germ cells are sometimes separated from the other cells early in ontogenetic development, Weismann came to believe that this separation signaled a qualitative difference between the two types of cells.[72] Referring to these findings Weismann wrote:

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[67] *Ibid.*, p. 89.

[68] A. Weismann, *The Evolution Theory* (London, 1904), Vol. 2, pp. 80-89. Darwin had offered a similar argument in *Origin of Species*: "I am surprised that no one has advanced this demonstrative case of neuter insects, against the well-known doctrine of Lamarck." *op cit.*, p. 242.

[69] *Ibid.*, pp. 97-98. Weismann traced the various insect castes to different genes in the queen, selection favoring the queen which produced the most harmoniously functioning colony.

[70] Spencer's essays are collected in H. Spencer, *Synthetic Philosophy* (London, 1898).

[71] *Ibid.*, p. 662. Modern research appears to have vindicated Spencer on this point. Thus Wilson observes: "By 1950 a modest amount of evidence had accumulated to indicate that the female castes are determined by environmental rather than genetic factors." See E. O. Wilson, *The Insect Societies* (Cambridge, 1971), p. 148.

[72] Churchill traces the development of Weismann's theory to certain ideas of Haeckel. See F. Churchill, "August Weismann and a Break from Tradition," J. Hist. Biol. 1 (1968), p. 101-102.

> "As their development shows, 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."[73]

Two ideas stand out in this summary statement of Weismann's position: (1) the immortality of the germ cells; (2) a qualitative difference between the germ cells and somatic cells. As we will see, these two postulates remained central to Weismann's understanding of heredity and he was to return to them again and again in his various writings on the subject. Weismann concluded this essay on a confident note:

> "We have an obvious means by which the inheritance of all transmitted peculiarities takes place, in the continuity of the substance of the germ cells, or germ-plasm. If, as I believe, the substance of the germ-cells, the germ plasm, has remained in perpetual continuity from the first origin of life, and if the germ-plasm and the substance of the body, the somatoplasm, have always occupied different spheres, and if changes in the latter only arise when they have been preceded by changes in the former, then we can, up to a certain point, understand the principle of heredity; or, at any rate, we can conceive that the human mind may at some time be capable of understanding it."[74]

It is interesting to note, however, that as of 1883 Weismann still hedged on whether the inheritance of acquired characters might play a minimal role in evolution: "Still we cannot exclude the possibility of such a transmission occasionally occurring, for, even if the greater part of the effects must be attributed to natural selection, there might be a smaller part in certain cases which depends on this exceptional factor."[75] Citing one of his own researches into the climatic variation of the coloration of butterflies, where he had induced dramatic changes in coloration by varying the temperature, Weismann confessed: "Even now I cannot explain the facts otherwise than by supposing the passive acquisition of characters produced by the direct influence of the environment."[76]

Weismann returned to the phenomena of heredity in an essay published two years later: "The Continuity of the Germ Plasm as the Foundation of a Theory of Heredity". Taking advantage of recent developments in cytology, Weismann argued that the hereditary material (the germ plasm) was of a complex material nature and that it was confined solely to the nucleus of the germ cell (the cytoplasm serving a nutritive function).[77] Weismann's researches into the embryogenesis of Hydromedusae, however, had demonstrated that germ cells do not as a rule become separated from the other somatic cells early in development, as he had earlier supposed. Weismann was thus forced to abandon his belief in the continuity of the germ cells, but he still managed to retain an emphasis on the continuity of the hereditary substance (germ plasm). Weismann accomplished this feat by hypothesizing that a small portion of the nucleus remained

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[73]Weismann, *Essays Upon Heredity*, p. 74.

[74]*Ibid*., p. 105.

[75]*Ibid*., p. 101.

[76]*Ibid*., pp. 100-101.

[77]*Ibid*., p. 181. Weismann thus became one of the intellectual fathers of the modern gene concept.

unchanged during embryonic development until the time of the formation of the germ cells. Weismann's discussion of this modification of his theory is as follows:

> "Those instances of early separation of sexual from somatic cells, upon which I have often insisted as indicating the continuity of the germ-plasm, do not now appear to be of such conclusive importance as at the time when we were not sure about the localization of the idioplasm in the nuclei. In the great majority of cases the germ-cells are not separated at the beginning of embryonic development, but only in some one of the later stages…We can only conclude that continuity is maintained, by assuming (as I do) that a small part of the germ-plasm persists unchanged during the division of the segmentation nucleus and remains mixed with the idioplasm of a certain series of cells, and that the formation of true germ-cells is brought about at a certain point in the series by the appearance of cells in which the germ-plasm becomes predominant."[78]

Apparent here is the great length to which Weismann was willing to go to salvage his belief in the unchangeableness of the germ-plasm during development, a belief which only makes sense with regard to his denial of the inheritance of acquired characters. Other writers, after all, had arrived at similar ideas of the continuity of the germ cells but all of them allowed for the possibility that external influences could affect the germ cells and thus facilitate an inheritance of acquired characters.[79]

Weismann's conception of development was further distinguished by the assumption that there was a qualitative division of the nucleus during ontogenetic development; i.e., that as embryonic development proceeds there results a successive diminution of the full complement of genetic information, the net result of which was the production of differentiated cells attributable to their qualitatively different nuclei. Weismann was thus a vocal opponent of the hypothesis that each cell in the body contained an identical nucleus, maintaining that it was "impossible that this substance can have the same constitution everywhere in the organism and during every stage of its ontogeny."[80]

This qualitative division of the nucleus during embryogenesis formed a cornerstone of Weismann's theory since it reinforced his belief that there was a fundamental difference between the germ cells and the somatic cells, the germ cells alone containing the complete genetic blueprint for the organism. This assumption, in turn, later led Weismann to deduce that inasmuch as the somatic cells contained a mere portion of the genetic material it followed that germ cells could only be produced by other germ cells. In support of this dictum Weismann referred to the common finding that a neutered animal is incapable of reproducing: "The familiar fact that the excision of the reproductive organs in all animals produces sterility proves that no other cells of the body are able to give rise to germ cells; germ plasm cannot be produced de novo."[81]

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[78]*Ibid.*, pp. 200-201.

[79]Prominent among such writers were Galton, Butler, and Hering. See, for example, the discussion in G. Romanes, *An Examination of Weismannism* (London, 1883), p. 63.

[80]Weismann, *op cit.*, p. 184. Weismann was apparently led to the belief in the qualitative division of the nucleus by the assumption that ontogeny recapitulates phylogeny; i.e., that as the primordial unicellular organism subsequently gave rise to the multicellular animals, so—it would seem to follow—does the zygote give rise through embryonic development to the various differentiated cells. *Ibid.*, p. 186.

[81]A. Weismann, *The Evolution Theory* (London, 1904), Vol. I, p. 411.

In addition to the perpetual continuity of the germ plasm, Weismann's original theory maintained that the germ plasm was completely impervious from external influences, whether from the body or the environment. The only heritable characters are those acquired from one's parents: "Only those characters which were potentially present in the germ of the parent can be transmitted to the succeeding generation."[82] Weismann's theory of heredity is unique in the history of biology in that it recognized no means whereby the germ cells might be modified during ontogenetic development (aside from nutritional influences of a minor sort, at least since the development of multicellular organisms). Such a theory is not only incompatible with the Lamarckian hypothesis, it is incompatible with the basic tenets of the modern synthesis as well (the modern view, of course, relies on accidental changes in the genetic code to provide the variation upon which natural selection is to act).

The attentive reader will have noticed that at this point Weismann would appear to have painted himself into a corner. If the germ plasm is immune to any and all changes from external influences, from whence derives the genetic variation upon which natural selection is to act? Weismann was not unaware of the ramifications of his view:

> "Individual variability forms the most important foundation of the theory of natural selection: without it the latter could not exist, for this alone can furnish the minute differences by the accumulation of which new forms are said to arise in the course of generations. But how can such hereditary individual characters exist if the changes wrought by the action of external influences, during the life of the individual, cannot be transmitted?"[83]

Weismann's answer to this all-important question stands as among the most bizarre ever offered by a biologist: genetic variation is to be traced to our one-celled ancestors! In Weismann's words:

> "The origin of hereditary individual variability cannot indeed be found in the higher organisms—the Metazoa and Metaphyta; but it is to be sought for in the lowest—in the unicellular organisms. In these latter the distinction between body-cell and germ-cell does not exist. Such organisms are reproduced by division, and if therefore any one of them becomes changed in the course of its life by some external influence, and thus receives an individual character, the method of reproduction ensures that the acquired peculiarity will be transmitted to its descendants. If, for instance, a Protozoon, by constantly struggling against the mechanical influence of currents in water, were to gain a somewhat denser and more resistant protoplasm…the peculiarity in question would be directly continued on into its two descendants, for the latter are at first nothing more than the two halves of the former. It therefore follows that every modification which appears in the course of its life, every individual character, however it may have arisen, must necessarily be directly transmitted to the two offspring of a unicellular individual."[84]

As this quote illustrates, Weismann conceded that Lamarckian inheritance governed variation at the unicellular level, and thus he went further than any Lamarckian in

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[82]Weismann, *Essays Upon Heredity*, p. 273.

[83]*Ibid*., p. 274.

[84]*Ibid*., p. 285.

attributing all genetic variation to the inheritance of acquired characters! Weismann summarized this train of thought as follows:

> "We are thus driven to the conclusion that the ultimate origin of hereditary individual differences lies in the direct action of external influences upon the organism. Hereditary variability cannot however arise in this way at every stage of organic development, as biologists have hitherto been inclined to believe. It can only arise in the lowest unicellular organisms; and…once…attained by these, it necessarily passed over into the higher organisms when they first appeared. Sexual reproduction coming into existence at the same time, the hereditary differences were increased and multiplied, and arranged in ever-changing conditions."[85]

Weismann's theory of the continuity of germ plasm represented a bold attempt to arrive at a synthesis of the facts of evolution, heredity, and development, and it generated an extensive amount of discussion and experimental research.[86] Within a few years of its publication it became clear that Weismann's grand theory was doomed to failure. As Mayr observed, it was the botanists who first led the attack against Weismann's theory:

> "The fact that in many kinds of plants a bud may be produced almost anywhere which can develop into flowers, as well as the fact that one can often reconstitute a new plant (with flower-producing germ cells) from a single leaf or other vegetative structure, completely refutes a strict separation of germ track and soma track."[87]

Biologists, similarly, observed that Weismann's dictum that germ cells could not be produced de novo from somatic cells was incompatible with the facts of regeneration.[88] It is well established, for example, that organisms from many different phyla can regenerate their reproductive organs, complete with fully functional germ cells. This ability is common among so-called lower forms such as planaria and hydra, of course, but as the anatomist F. W. Jones noted, it can be found among the higher phyla as well. With reference to Weismann's famous dictum, Jones observes:

> "It is owing to the persistence of his teaching that the historical and anatomical separation of the sex cells from soma cells is still insisted on in most recent works…It is, however, quite certain that this basal thesis stands in need of revision. So much are germ cells akin to the body cells that, far from their aloofness being shown by their specialized and independent origin, we must now admit that their appearance in development is often suspiciously late, and that they may be developed de novo, even in adult animals, from pre-existing soma cells. Recent experiments have shown that when both ovaries, their capsules, portions of the Fallopian tubes, the fat bodies and portions of the surrounding tissues are removed from adult mice, new ovaries containing new sex cells may be developed. These new ovaries perform their normal function of re-establishing the oestrous cycle, even leading to normal pregnancy;

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[85]*Ibid*., p. 286. Here Weismann refers to the direct effects of the environment which, although only a minor factor in Lamarck's overall view of evolution, was assigned a prominent role in the evolution of protozoans in Lamarck's system as well.

[86]For a glimpse into the debate caused by Weismann's theory see G. Romanes, *An Examination of Weismannism* (London, 1883).

[87]Mayr, *op cit*., p. 703.

[88]A. Weismann, *Essays Upon Heredity, op cit*., p. 198. Kammerer raised this objection, among others. See the discussion in Kammerer, *op cit*., pp. 125-126.

> and histologically they are in every way typical of normal ovaries…It is difficult, in the face of these facts, to give full acceptance to the doctrines of Weismannism."[89]

Weismann's view of development suffered a similar fate. Although some early experiments seemed to support Weismann's theory of a qualitative division of the nucleus during ontogenetic development, later research showed that this view was untenable.[90] Thus, whereas Weismann had argued that the first segmentation of the zygote gave rise to two blastomeres with only half the information necessary to produce a complete embryo, the classic experiment of Driesch in 1891 showed that upon isolation each of the first two blastomeres of a sea urchin could produce a complete embryo.[91] In 1895, Zoja obtained perfect embryos from blastomeres of the eighth and sixteenth stages. Years later the cytologist E. B. Wilson was led to remark:

> "These experiments render highly improbable the hypothesis of qualitative division in its strict form, for they demonstrate that the earlier cleavages, at least, do not in these cases sunder fundamentally different materials, either nuclear or cytoplasmic, but only split the eggs up into a number of parts, each of which is capable of producing an entire body of diminished size, and hence must contain all of the material essential to complete development."[92]

Modern concepts of heredity, in fact, proceed upon the assumption that all of the cells in a given organism are genetically equivalent. Robert McKinnell, a pioneer in cloning research, summarizes the modern position as follows:

> "All concepts regarding control of gene expression have the prerequisite of equivalence of genetic content of somatic nuclei. I believe that the blastomere separation studies available as of this writing support the view that there are probably no fundamental differences between determinant and determinate eggs and the molecular mechanisms underlying differentiation are likely to be the same among all nucleated organisms."[93]

This finding raises an important question for all theories such as Weismann's which seek a genetic explanation of development: if all the cells of a given organism are genetically equivalent what determines whether a particular cell becomes a germ cell or a somatic cell? While a conclusive answer to this question remains elusive, it is clear that the cytoplasm plays a fundamental role in the determination of the fate of a particular cell. The development of germ cells, as McKinnell points out, involves the selective introduction of non-nuclear factors into the cell body:

> "The germ line and its special cytoplasm are still being studied many years after Weismann published his now discarded theory…Briefly, it can be shown that the early segregating primordial germ cells are de facto germ cells not because of nuclear peculiarities but because of special cytoplasm (at least in Drosophilia and certain frogs) that is rich in mitochondria and stains as RNA. Thus Weismann, who thought that germ cells were different from

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[89]F. W. Jones, *Man's Place Among the Mammals* (London, 1929), p. 27.

[90]In 1888, for example, in the famous experiment of Roux, a half embryo resulted upon the destruction of one cell of a two-celled embryo, an apparent confirmation of Weismann's hypothesis of qualitative division. This experiment, however, was later found to be flawed.

[91]Weismann, *op cit*., p. 199. See also Weismann's *The Germ Plasm* (New York, 1902), p. 32.

[92]E. B. Wilson, *The Cell in Development and Inheritance* (New York, 1925), pp. 409-410.

[93]R. McKinnell, *Cloning* (New York, 1978), p. 8.

> somatic cells because of an undiminished genome, was wrong. The uniqueness of germ cells must be attributed to cytoplasmic determinants."[94]

To go on finding fault with Weismann's theory of the continuity of the germ plasm seems a bit like beating a dead horse. In nearly every instance in which it has been possible to test Weismann's theory it has been found to be in error. The germ cells' peculiar manner of development does not reflect a superior or undiminished nucleus, nor does it preclude their stimulation by external factors; the nucleus does not undergo a qualitative division during embryonic development; the cytoplasm is not devoid of genetic information, nor does it play a passive role during differentiation; excision of the reproductive organs does not preclude the production of germ cells; etc.

In all fairness to Weismann, several of these objections to his theory became known during his lifetime and he immediately set about revising his original formulations. Thus Weismann was eventually forced to accept the fact that external influences could effect changes in the germ cells. Here Weismann acknowledged changes due to the infection of the genome by foreign bacilli (such as that responsible for syphillus), as well as changes attributable to environmental stimuli such as temperature.[95] Weismann sought to accommodate this evidence by postulating that external influences could only produce variations that were accidental and non-adaptive in nature. This concession, however, would appear to have obviated Weismann's earlier critique of the theoretical impossibility of Lamarckian inheritance, as his denial of the inheritance of acquired characters could really only be sustained if all external influences upon the germ cells were ruled out (as in his earlier system). Once allow the infection of the germ cells by extraneous agents like bacilli and the door is opened to pangene-like factors allowing for adaptive changes. Indeed Weismann conceded that such factors were operable in plants, where plastids routinely penetrate the cell wall and become heritable.[96] Weismann maintained, however, that such cytoplasmic factors were impossible in animals, yet another false deduction precipitated by his unwillingness to accept the possibility of the inheritance of acquired characters.[97]

Of all Weismann's revisions the most telling, perhaps, is the abandonment of the "all-sufficiency" of natural selection as a mechanism of evolutionary change. Now

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[94]*Ibid*., pp. 6-7.

[95]A. Weismann, *Evolutionary Theory*, *op cit*., p. 68. It was via the latter factor that Weismann sought to explain the few remaining problems seemingly requiring a belief in the inheritance of acquired characters, such as his earlier researches with regard to temperature-induced changes in the coloration of butterflies. Now Weismann would argue that these induced variations only simulated Lamarckian inheritance, involving in reality parallel changes in the body and genome, which had been similarly and simultaneously modified. A. Weismann, *The Germ Plasm* (New York, 1902), p. 401.

[96]Here Weismann conceded that the introduction of plastids into the plant cell constituted an inheritance of an acquired character.

[97]*Ibid*., p. 28. See also A. Weismann, "A Reply to Prof. Vines," Nature 11 (1890), p. 323. The fact is, however, that cytoplasmic factors play an important role in the reproduction of animals as well. To take but one example, a key role in the spatial organization of the future embryo is believed to be attributable to the selective infusion of extraneous cytoplasmic material into the developing egg cell. W. Gehring, "The Molecular Basis of Development," *Scientific American* 253: 4 (Oct., 1985), pp. 154-156.

Weismann could speak of "the obvious gaps and insufficiencies of the Darwinian theory."[98] Among other things, Weismann had come to agree with Spencer and the Lamarckians that selection—even if supplemented by panmixia—could never account for such phenomena as the complete reduction of organs no longer of use.[99] The problem, as Weismann acknowledged, was that in such cases there was no satisfactory explanation why the respective genetic variations continued in the direction of diminished size.[100] To solve this problem Weismann proposed his theory of germinal selection, whereby a struggle is envisaged as occurring amongst the hereditary material (now envisaged as miniature living beings called biophors) for nutrition.[101] Here the non-useful character is literally starved out of existence.[102]

It is not without interest that the father of Neo-Darwinism was forced to question the efficacy of natural selection as an explanation of evolution. Weismann's later views, not surprisingly, are rarely cited by modern writers, apparently because of the embarrassment caused by his lack of faith in natural selection and attribution of vital qualities to the particles of heredity. Mayr, in his analysis of Weismann's career, barely touches upon these later developments, offering instead the following disclaimer:

> "Like all imaginative pioneers, Weismann was quite open-minded and never hesitated to revise his theories when he thought this was required by new evidence. Unfortunately, his revisions, particularly those published after 1890, were not always improvements, when seen in the light of modern knowledge."[103]

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[98]A. Weismann, *The Evolutionary Theory*, p. 9.

[99]*Ibid.*, p. 115.

[100]*Ibid.*, p. 116.

[101]*Ibid.*, pp. 117-119. According to Weismann's final formulations on evolution, this struggle among biophors accounted at once for the origins of variation and for the eventual preservation or disappearance of a particular character. The importance of this new found factor is apparent in the following quote: "It is, then, germinal selection alone which brings about the presence of a majority of ids [chromosomes] with determinants varying in the same direction, and personal selection has no part in the transformation of the species." *Ibid*, p. 136

[102]Weismann's assignment of vital qualities to the nuclear determinants seems attributable to his unwillingness to accept that nuclear factors might be modified during development, a circumstance which could be used to support the hypothesis of the inheritance of acquired characters. Thus Weismann criticized those theorists like Delage who would attribute the phenomena of heredity to chemical substances lying in the nucleus since "chemical substances are not vital units, which feed and reproduce, which assimilate and which bear a charm against the assimilating power of the surrounding protoplasm. They would necessarily be modified and displaced in the course of ontogeny." *Ibid.*, p. 401.

[103]Mayr, *op cit.*, p. 699. Mayr's resume of Weismann's contributions, as might be expected, is a glowing one: "One of the great biologists of all time. He was unique among all those who worked on cytology, development, and inheritance in the last century by being an uncompromising selectionist…From the point of view of scientific methodology, again, he was notable for his period in his careful, rational analysis of every problem he encountered. When he wanted to interpret a given phenomenon or process, he attempted to reason out all the possible solutions. Almost invariably this included the solution that is now considered to be the right one. Owing to the insufficient and sometimes even faulty information available at his time, Weismann himself sometimes chose an alternative that is now rejected. This does not in the slightest diminish the magnitude of his intellectual achievement. He never made a hasty decision but always first surveyed the entire field of possible solutions. His was the first truly comprehensive theory of genetics and his theorizing prepared the way for the research of the entire next generation."

ACQUIRED CHARACTERS

Weismann's original formulation of the theory of the continuity of the germ plasm underscores the need—and inherent difficulty—of arriving at a satisfactory definition of an acquired character. The definition of an acquired character, like that of mutation, fitness, and many other fundamental concepts in evolutionary theory, has evolved through time. The historian Peter Bowler suggests that it is possible to distinguish four kinds of acquired characters: (1) those resulting from use-inheritance; (2) those resulting from an automatic response to the environment, as in the production of long hair to cold weather (such adaptations are perhaps best thought of as reflecting the self-regulatory capacity of living forms); (3) direct environmental influences upon the germ cells, as via temperature or radiation; (4) mutilations.[104] To this list I would add those characters resulting from the incorporation of foreign agents, whether these agents be in the form of viruses, organelles, symbionts, or other organic factors. The reason for including this factor will become apparent in a following section.

Ultimately, of course, all characters are acquired, provided one believes in evolution and not divine creation.[105] Hence all biological characters were acquired at some point during phylogeny, no matter how the character was generated. In Weismann's early system, for example, all characters were acquired at some stage prior to the development of multicellular animals via direct environmental effects.

Weismann's denial of the inheritance of acquired characters applied strictly to multicellular life forms and was based on the assumption that no new changes could arise in the germ-plasm once that level of development was reached.[106] A chemically induced mutation, it should be noted, would be an acquired character according to Weismann's original formulations. Years later, upon the discovery of radioactive and chemical mutagens, Lamarckian critics argued that such mutations proved Weismannism false, at

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[104]Bowler, *op cit.*, pp. 62-65. The discussion of Lamarckian forms of evolution has suffered from the failure of the respective proponents to keep separate the inheritance of the direct effects of the environment from the inheritance of the indirect effects of the environment (the classical Lamarckian inheritance, resulting from behavioral responses to environmental contingencies). Many Neo-Lamarckians, particularly the American school of paleontologists represented by Cope, Osborne, and Hyatt, held that acquired characters directly induced by the environment were of prime importance in evolution. As an example of this phenomenon we might consider the coloration of insects. Neo-Lamarckians held that coloration was primarily the result of the direct influence of light, which effected parallel changes in the body and the genome. Here the environmental stimulus is directly induced on the evolving organism, in contrast to classical Lamarckian inheritance which makes the animal respond indirectly to the stimulus via the mediation of behavior. For a discussion of recent evidence bearing on this question see C. Cullis, "Environmentally induced DNA changes," in *Evolutionary Theory: Pathways into the Future*, ed. by J. Pollard (New York, 1984), pp. 203-216.

[105]One other exception besides creationism might be mentioned; namely, preformationism. This belief holds that originally ideal types successively degenerate during phylogeny resulting in the various life forms. Here there is no true evolution or acquired characters; rather an unfolding of an originally complex creation (this is the original meaning of the word evolution, by the way). Weismann's view of development, for example, betrays the definite influence of the preformationist position.

[106]"Only those new characters can be called acquired which owe their origin to external influences." Weismann, *op cit.*, p. 258.

least in its strict form. (And indeed it is well-known that these mutations were originally regarded as being incompatible with Darwin's theory of evolution).[107] Leaders of the Neo-Darwinian Synthesis, however, such as Muller, Fisher, Dobzhansky, Simpson, and Huxley latched on to these mutagenic changes afflicting the genome and suggested that here at last was a source of the small genetic variations which they believed were necessary to fuel evolution. Neo-Darwinism thus came to be associated with genetic variation that was of an accidental, non-directed nature. Lamarckian inheritance, in contrast, came to signify only adaptive or directed genetic variation. While this distinction is somewhat arbitrary we will adhere to it here since this has come to be the general sense in which the term acquired character is understood.

An acquired character is thus any character—be it a change in behavior, form, or function—which occurs in the life of an individual organism. Here it may be useful to approach this issue from the vantage point of modern information theory. To oversimplify the situation somewhat, an organism at any given point in time can be said to consist of a generally fixed set of characters or biological information. An inheritance of acquired characters can be said to occur if and when this fixed set of information is supplemented by new information (regardless of the source) which subsequently becomes heritable.[108] An accidental change in DNA, whether resulting from environmental mutagens or errors in transcription, would—according to this definition—correspond to background noise rather than information and thus would not be considered an example of Lamarckian inheritance.

WEISMANNISM AND THE MODERN SYNTHESIS

Despite the failure of Weismann's theory of heredity, vestiges of his ideas continue to exert a formidable influence upon the formulations of modern biologists. How else but upon Weismann's theory of the unchangeable germ plasm can one understand the curious statement of Mayr to the effect that the problem with Lamarckian theories of evolution is that they "deny the complete constancy of the genetic material that we now know to exist."[109] Mayr's statement is so blatantly false as to be laughable and indicates a lack of ability to consider the issue of Lamarckism objectively.

Weismann's theory of a distinction between the germ cells and somatic cells, similarly, together with its insistence upon a one-way information flow between the germ plasm and somatic cells, has a modern correlate, albeit in a somewhat mutated form: the so-called central dogma of Watson and Crick. (Watson and Crick, as is well-known, revolutionized the science of heredity when they unraveled the helical structure of DNA. Since their researches it has generally become accepted that DNA serves as the master

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[107] Bowler, *op cit*., pp. 198-200.

[108] A further distinction could be made between information obtained from within the body of the organism (i.e. endogenous incorporation) and information obtained from without the organism's body (exogenous incorporation).

[109] E. Mayr, *The Evolutionary Synthesis*, p. 15.

molecule of the cell, as the sole bearer of hereditary information).[110] The central dogma, when it was first put forward in the mid-fifties, was commonly taken to mean that there is a one-way information flow between DNA and its products (RNA, proteins, etc.)[111] The opinion of Jacques Monod, a Nobel-prize winning biologist, may be taken as representative of the majority view at the time: "It is not observed, nor indeed is it conceivable, that information is ever transferred the other way around…)"[112]

If DNA is indeed the sole source of bio-chemical inheritance, and if the central dogma is true, Lamarckian inheritance (at least as traditionally understood) would be ruled out. In the mid-sixties Maynard Smith summed up the significance of the central dogma for evolutionary theorists: "The greatest virtue of the central dogma is that it makes clear what a Lamarckian must do—he must disprove the dogma."[113]

In 1970 the scientific world was stunned when Howard Temin announced the discovery of an enzyme which enabled RNA to synthesize its own DNA.[114] Originally found in retrovirsuses known to induce cancer tumors, the enzyme in question—reverse transcriptase—has since been found in many different animals, and is believed to be a fundamental component of normal cells. Temin's research initiated a revolution in the understanding of the workings of the genome and in 1975 he was awarded the Nobel prize.

Temin's researches confirm that there is a two-way flow of information—at least between DNA and RNA. This finding is of decisive importance to Lamarckism not only for its import with regard to the sanctity of the central dogma, but because Lamarckian inheritance requires that the genome receive feedback from its products. Thus, the possibility arises that RNA might direct the creation of DNA in line with the needs of the evolving organism. Temin himself theorized that RNA-directed synthesis of DNA plays a fundamental role in differentiation (the proto-virus theory).[115] It is Temin's belief that retroviruses (or retrovirus-like agents) may have evolved to serve a functional role as intracellular messengers, conveying genetic information between the respective cells of an organism. Temin has also suggested, finally, that an infection of the germline by one of these viral agents might allow for the inheritance of acquired characters:

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[110]This thesis, however, a prime example of the reductionist position so apparent in Neo-Darwinism itself, is almost certainly in need of revision. See B. Commoner, "Failure of the Watson-Crick theory as a chemical explanation of inheritance," *Nature* 220 (1968), pp. 334-340.

[111]While the original formulation of Crick left the door open to the possibility that RNA might convey information to DNA, this possibility was generally regarded as unlikely by molecular geneticists. Thus Temin observed: "Although Crick's original formulation contained no proscription against a 'reverse' flow of information from RNA to DNA, organisms seemed to have no need for such a flow, and many molecular biologists came to believe that if it were discovered, it would violate the Central Dogma." H. Temin, "RNA-Directed DNA Synthesis," *Scientific American* 226 (1972), p. 25.

[112]Quoted in P. Grasse, *Evolution of Living Organisms* (New York, 1973), p. 221.

[113]J. Smith, *The Theory of Evolution* (Middlesex, 1966), p. 66.

[114]For a discussion of this research see H. Temin, "The DNA Provirus Hypothesis," *Science* 192 (June, 1976), pp. 1075-1080.

[115]H. Temin, "Guest Editorial," *J. Natl. Cancer Institute* 46 (1971), p. iv.

> "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."[116]

With the notable exception of Steele and Gorczynski, Temin's findings have not caused biologists to reconsider the possibility of Lamarckian inheritance. Witness the following statement of Monod, the very man who claimed that a reverse flow of information from RNA/proteins to DNA was inconceivable:

> "The old idea of acquired characters, which had been proposed by Lamark [sic], not only has never been verified, as you probably all know, but in fact is completely incompatible with all of what we know of the whole structure of transfer of information. First, the spontaneous nature of mutation is incompatible with such an idea and second, we know that this sequence of transfer of information is essentially irreversible. Here, I think, I must correct a wrong idea that has been spreading for the past three or four years. It was discovered some years ago that in some cases, the transcription step from DNA to RNA works in the reverse direction. That is nothing surprising. This is a very simple step and even by the basic principle in physical chemistry of the reversability of microscopic events, it could be predicted that such events could occur. They do occur, indeed, but this must not be taken to mean that information from protein could possibly go back to the genome. I think, in spite of some hesitation even by some very distinguished colleagues, I am ready to take any bet you like that this is never going to turn out to be the case."[117]

What an amazing turnabout! Once "inconceivable," the reverse translation of information from RNA to DNA is suddenly "nothing surprising" and might easily have been predicted!

THE WORK OF STEELE AND GORCZYNSKI

The next major development on the Lamarckian front occurred in 1979, with the appearance of Steele's *Somatic Selection and Adaptive Evolution.* It is Steele, perhaps, who has done more than anyone else to establish the inheritance of acquired characters on a firm genetic basis. Steele's hypothesis, briefly, is as follows. During the course of an organism's life mutations are constantly arising in its somatic cells, some of which might prove beneficial to the organism and aid it in adapting to its environment. In the case of immunological response, for example, the body of an animal generates a specific antibody to neutralize the invading antigen. The generation of this antibody is believed to be a random process, i. e., mutational in nature, and it is known that such mutated cells soon proliferate throughout the blood (somatic selection). Invoking the ubiquitous presence of Temin's retroviruses, Steele speculates that a virus might pick up some of the genetic material responsible for the adaptive response (probably as RNA rather than DNA) and transport it to the germ line, at which time it would become incorporated into the genome and be passed on to the animal's progeny.

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[116]Ibid., p. vi.

[117]J. Monod, "On the Molecular Theory of Evolution," in *Problems of Scientific Revolution* (Oxford, 1975), ed. by R. Harre, p. 20.

The most significant aspect of Steele's hypothesis is that it is built upon established data. Thus it is known that viruses are capable of incorporating genetic material from somatic cells and of infecting the germ line.[118] The question is how frequently does such a process occur in nature? Certainly it seems to be asking a lot to expect evolution to proceed largely because of the fortuitous infection of the genome by foreign agents such as retroviruses.[119]
Steele suggests, however, that it is the adaptive benefits conferred by retroviruses that accounts for their widespread prevalence. In this belief Steele is again extrapolating from the views of Temin, who speculated that retroviruses—such as those responsible for certain types of cancer—are simply the pathogenic offshoots of normal genes which otherwise play a key role in cellular differentiation.

Steele followed the presentation of his theory with the announcement of experiments allegedly showing the inheritance of acquired characters.[120] These experiments, performed in collaboration with R. Gorczynski, appeared to show that upon inoculation with foreign cell matter rabbits could pass on an acquired immunological response to their offspring. As the authors pointed out, similar results had previously been obtained by other research teams.[121]

Subsequent attempts to repeat these experiments failed, however, for what reason(s) is not yet clear. A major controversy ensued, yet to fully dissipate. Suffice it to observe here that the field of immunology is a complicated one, with a variety of interpretations being possible.[122]

It is important to recognize, however, that Steele's hypothesis, while controversial, does not represent the challenge to the modern synthesis that the more orthodox Lamarckian theory would. This much is clear from the various remarks of commentators on the controversy. Bowler, for example, has observed:

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[118]See the lengthy discussion in E. J. Steele, *Somatic Selection and Adaptive Evolution* (Toronto, 1979), pp. 78-81.

[119]Temin, asked to offer an opinion with regard to Steele's hypothesis, commented that a major problem facing it is how the virus becomes incorporated into the host's genome: "There is apparently no particular specificity in where the viruses insert their passenger DNA into the genome. This is obviously important for the hypothesis, and it therefore poses a severe difficulty." See R. Lewin, "Lamarck Will Not Lie Down," *Science* 213 (July 17, 1981), p. 317. That viruses play a fundamental role in evolution was also expressed by N. Anderson, "Evolutionary Significance of Virus Infection," *Nature* 227 (September 26, 1970), pp. 1346-1347.

[120]R. Gorczynski & E. Steele, "Inheritance of acquired immunological tolerance to foreign histocompatibility antigens in mice," *Proc. Natl. Acad. Sci.* USA 77 (May 1980), pp. 2871-2875; "Simultaneous yet independent inheritance of somatically acquired tolerance to two distinct H-2 antigenic haplotype determinants in mice," *Nature* 289 (Feb. 19, 1981), pp. 678-681.

[121]E. Steele & R. Gorczynski & J. Pollard, "The Somatic Selection of Acquired Characters," in *Evolutionary Theory: Pathways into the Future*, ed. by J. Pollard (New York, 1984), pp. 226.

[122]It is important to note that the experiments of Gorczynski and Steele could be valid and Steele's theory invalid (i.e., more traditional Lamarckian inheritance might be involved). Or, alternatively, both could be valid but unrelated so far as these particular experimental results are concerned.

> "Steele's ideas are not a threat to the central dogma of molecular biology, nor do they really conflict with the existing framework of evolution theory. Apart from the fact that the theory requires a quasi-Darwinian mechanism within the body to produce new genetic material, it is not intended to be more than an addition to natural selection. If valid, the new mechanism merely would speed up evolution by allowing a more rapid adjustment of bodily structure to new habits adopted by the organism."[123]

Richard Dawkins, known best for his theory of the selfish gene, perhaps the closest modern counterpart to Weismann's theory of the continuity of the germ plasm, notes that Steele's theory bears more resemblance to Darwin's pangenesis hypothesis than to anything that Lamarck wrote, a point acknowledged by Steele.[124] Dawkins concludes:

> "The very essence of Steele's hypothesis is that the adaptive improvement comes about through selection of initially random variation. It is about as Darwinian a theory as it is possible to be."[125]

While both Bowler and Dawkins make valid points, it is clear nevertheless that Steele's theory marks a radical departure from Neo-Darwinian principles. It postulates that Weismann's barrier between the germ cells and somatic cells is routinely penetrated and that this penetration allows for the genome's direct acquisition of adaptive information about the environment. Such a fundamental challenge to the Neo-Darwinian position cannot be assimilated as easily as Bowler and Dawkins would have us believe. The bitter controversy which has attended Steele's work is sufficient proof of this point.

THE WORK OF CAIRNS AND HALL

In a paper submitted to the prestigious *Nature*, Cairns et al., describe a series of experiments in which bacteria displayed a remarkable ability to adapt to a variety of substrates. Briefly, the authors raised bacteria in a medium in which lactose served as the only energy source (lactose was chosen because the bacterial subjects of the experiment were known to be incapable of using this sugar as an energy source). Within a short period of time, however, it was discovered that bacteria had indeed developed the ability to process lactose, presumably because a mutation from Lac- to Lac + had occurred. It was shown, moreover, that this genetic change only occurs in the presence of lactose. The authors concluded that bacteria apparently possess the ability to generate precisely those "mutations" which allow them to adapt to their particular environment. This, of course, is exactly what one would expect upon the Lamarckian theory of evolution, in which the genome changes in accordance with the needs of the organism.

That the adaptations of the bacteria involve an inheritance of acquired characteristics is considered by the authors. Cairns points out, moreover, that these experiments also cast doubt on the final bastions of Neo-Darwinism: the spontaneousness of mutations and the supposed impossibility of any communication between proteins and DNA (remember Monod's statement in an earlier section). The discussion of Cairn's et al is so important it will be quoted here at some length:

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[123]P. Bowler, *Evolution: The History of an Idea* (Berkeley, 1984), p. 321.

[124]R. Dawkins, *The Extended Phenotype* (San Francisco, 1984), p. 167.

[125]*Ibid*., p. 168.

> "The main purpose of this paper is to show how insecure is our belief in the spontaneity (randomness) of most mutations. It seems to be a doctrine that has never been properly put to the test. We describe here a few experiments and some circumstantial evidence suggesting that bacteria can choose which mutation they should produce. But we realize that this is too important an issue to be settled by three or four rather ambiguous experiments…Curiously, when we come to consider what mechanism might be the basis for the forms of mutation described in this paper we find that molecular biology has, in the interim, deserted the reductionist. Now, almost anything seems possible. In certain systems, information freely flows back from RNA into DNA; genomic instability can be switched on under conditions of stress, and switched off when the stress is over; and instances exist where cells are able to generate extreme variability in localized regions of their genome. The only major category of informational transfer that has not been described is between proteins and the messenger RNA (mRNA) molecules that made them. If a cell discovered how to make that connection, it might be able to exercise some choice over which mutations to accept and which to reject.
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> "Since this is the kind of versatility and adaptability we seem to be seeing in these experiments with E. coli, it is worth considering briefly how such a connection might be made. In a very direct way, the cell could produce a highly variable set of mRNA molecules and then reverse-transcribe the one that made the best protein…"[126]

The authors go on to discuss several biochemical possibilities whereby proteins might be monitored, concluding that such processes "might provide a mechanism for the inheritance of acquired characteristics."[127] Note here that Cairns et al., consider the possibility that information does indeed flow "backwards" from proteins to RNA to DNA. This hypothesis, if confirmed, would appear to obviate once and for all any theoretical objections to Lamarckian forms of inheritance.

Since the publication of the paper by Cairns et al., word has come of other equally revolutionary findings from yet another laboratory. In this series of experiments, Barry Hall suggests that bacteria can rearrange portions of their genome in response to a novel environment.[128] Hall's findings are perhaps even more radical than Cairns' inasmuch as they suggest that more than one "mutation" can be directed in a coordinated fashion to satisfy the needs of the bacteria.

Hall discovered that in order to adapt to an environment laced with salicin, bacteria first responded by the excision of one gene (known as IS103) afterwhich followed a change in another gene (bglR), the latter known to be involved in the processing of salicin. Hall concluded that the excision of IS103 occurred in apparent anticipation of the subsequent change in bglR even though it conferred no adaptive advantage by itself.[129] The adaptive value of IS103, apparently, is only apparent upon subsequent activation of bglR, the two genes together allowing the bacteria to adapt to salicin. These results, according to Hall, seem to indicate that gene change is susceptible to regulation by environmental factors:

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[126]J. Cairns & J. Overbaugh & S. Miller, "The Origin of Mutants," *Nature* 335 (1988), p. 145.

[127]*Ibid*., p. 145.

[128]B. Hall, "Adaptive evolution that requires multiple spontaneous mutations," *Genetics* 120 (December, 1988), pp. 887-897.

[129]Indeed Hall states that the excision of IS103 is only detected when it creates the potential for the subsequent advantageous mutation. *op cit*., p. 894

> "We now take for granted the notion that gene expression is regulated, i.e., subject to modulation by environmental conditions…We now have to examine the notion implied by these results, that mutation, like other biological processes, is subject to regulation by environmental factors."[130]

Hall's conclusion is carefully worded. The intent, apparently, is not to unduly alarm his fellow scientists, most of whom swear allegiance to the Neo-Darwinian paradigm. The import of Hall's work is clear nevertheless. A fundamental postulate of Neo-Darwinism—that mutations occur at random with respect to the needs of the organism and the nature of the environment—is apparently on the verge of being overthrown. A more threatening development for the fate of the modern synthesis is difficult to imagine.[131]

It is of interest here to note that this remarkable adaptability of bacteria has been known for some time, overlooked no doubt because it might arouse the spectre of Lamarck from his pauper's tomb. C. H. Waddington, for example, certainly seems to have had something similar in mind over thirty years ago, when, in a discussion of the possibility of Lamarckian inheritance, he observed:

> "Recent developments have made it somewhat easier to envisage mechanisms by which such effects might conceivably operate. In particular, it has been found that in many micro-organisms, such as yeasts and bacteria, the presence of some unusual substrate may provoke the formation of an appropriate enzyme; and there are some reports of the synthesis of such adaptive enzymes in higher organisms. The mechanism of the process is still obscure, but its reality seems beyond question. Now genes can be considered to be enzymes, or at least to be in many ways similar to the more typical cellular enzymes…one would not, perhaps, be too much astonished if it should be found that some metabolic 'opportunity' available in the cell might tend to induce a gene mutation to an allele which in some way fitted it."[132]

Although it would be premature to assume that the findings of Cairns et al., and Hall reestablish Lamarckian inheritance as a general principle of heredity—much more research on a variety of animals needs to be done before such a claim could possibly be made—such findings support the possibility that Lamarckian inheritance is a real phenomenon even if questions remain concerning its extent and importance in evolution.[133]

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[130]*Ibid.*, p. 895.

[131]Witness Dawkins' recent confession: "To be painfully honest, I can think of few things that would more devastate my world view than a demonstrated need to return to the theory of evolution that is traditionally attributed to Lamarck. It is one of the few contingencies for which I might offer to eat my hat." See Dawkins, *op cit.*, pp. 164-165.

[132]Waddington, *The Strategy of the Genes*, (New York, 1957), p. 180.

[133]The research of Cairns and Hall raises an important task facing modern biologists; namely, that of arriving at a satisfactory definition of mutation. As understood by modern geneticists, a mutation connotes an accidental change in DNA; specifically a change in a base coding for an amino acid or a restructuring of a chromosome. Neo-Darwinism holds that such changes in league with selection determine the course of evolution. The research of Cairns and Hall, however, suggests that mutation may be a directed process, subservient in part to the needs of the evolving organism. This is something quite different and is exactly what Lamarckians such as myself have been insisting upon for some time. The very phrase employed by Cairns—"that bacteria can choose which mutations they produce"—conjurs up the memory of Lamarck. Hence I would like to propose that some new term be found to describe directive genetic change, mutation

BACTERIA, SYMBIOSIS, AND THE INHERITANCE OF ACQUIRED CHARACTERS

In the reconstruction of phylogenies of genes and their products, geneticists routinely make the assumption that one can extrapolate from bacterial genetics to the genetics of higher life forms and indeed there are solid reasons for doing so. Hence it is worth asking the following question: If Lamarckian modes of inheritance are operable in bacteria, as the research of Cairns et al., and Hall seems to suggest, is there any good reason why such processes should not occur in higher life forms as well? Is it likely that a process which would allow a bacterium to directly adapt to its environment would be lost by its phylogenetic heirs? Does not the theory of natural selection imply that such a mechanism would be subject to intense selection and in all probability be maintained? Put another way, would an organism equipped with a system allowing for Lamarckian inheritance be inclined to give up such a system in exchange for one relying on accidental mistakes in the genetic code? Surely the onus of proof must rest with the theorist who would make such a judgment.

Most evolutionists accept that prokaryotes (those organisms which lack a nucleus, such as bacteria) constituted the primeval ancestors of both the Plant and Animal kingdoms and thus of all known life forms on Earth.[134] Despite this generally acknowledged relationship it is easy to overlook the pivotal role played by microorganisms in the evolution of life on Earth. As Margulis points out, some of the most fundamental evolutionary steps occurred among bacteria: "All of the great innovations in the evolution of cells occurred before the first animals, plants, and fungi developed."[135] The development of photosynthesis and many other metabolic firsts, for example, had its origin in bacteria. If any of these developments could be proved to have taken place via Lamarckian inheritance this alone would be important news.

A decisive step in the evolution of life on Earth was the development of the cell's various organelles, such as mitochondria and chloroplasts. How these organelles came to be a part of the primeval cell is a much-debated question. The conventional view is that the organelles became differentiated from the nucleus during the course of evolution. An alternative view, one that is rapidly gaining acceptance, is that the various organelles first became incorporated into the bodies of ancestral eukaryotes as separate life forms (i. e. as other bacteria), after which a symbiotic relationship developed and persisted to the point at which it is now difficult to recognize their separate origins.

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being inadequate given its past history and tendency to connote accidental processes (the term directed mutagenesis had been suggested in reference to Cairn's results). Since the type of gene change envisaged by Cairns and Lamarckians is the product of organismic autoregulation perhaps the term biotation would be appropriate. Whatever the eventual term chosen a clear distinction should be made between a genetic change which is of a directed, adaptive nature and those changes which are accidental in origin and non-adaptive in nature. See Cochrane, *op cit.*, pp. 234-248.

[134]L. Margulis, *Symbiosis in Cell Evolution* (San Francisco, 1981), p. 40.

[135]*Ibid.*, p. 14.

There is a good deal of evidence favoring the symbiotic origin of organelles. It is possible to demonstrate, for example, that the ribosomal RNA of mitochondria is more similar to the RNA of certain bacteria than to the RNA of the cytoplasm of the host cell.[136] Further evidence consistent with the symbiotic origin of organelles is the fact that there are numerous examples of microbial symbionts which are transmitted independently of the nucleus. The well-known kappa particles of paramecia, which render their hosts killers of kappa-less paramecia, are actually Gram-negative bacteria.[137] Here Margulis was led to observe:

> "Most, perhaps all, nonnuclear (non-Mendelian) eukaryotic genetic factors, many known to be inherited uniparentally, have symbiotic or viral origins. Some examples are variegated plant plastids, the Drosophilia sex-ratio 'gene', now known to be a population of symbiotic bacteria, u particles in paramecia, the genetic determinant of lysine biosynthesis in Crithidia oncopelti, y particles in Blastocladiella, and perhaps even the B chromosomes of maize."[138]

If the symbiotic theory of the origin of certain organelles is valid it stands to reason that the various symbiotic relationships entered into by the primordial eukaryotic organism allowed it to acquire new characters directly, overnight as it were. The incorporation of mitochondria-like bacteria, for example, preadapted the ancestral eukaryote for oxidizing environments. The incorporation of chloroplast-like bacteria, similarly, allowed the eukaryotes to secure food by photosynthesis in the absence of other nutrients. Each of these developments allowed the ancestral eukaryote to exploit new environments and set the stage for the proliferation of new life forms.

A decisive issue for us is how to explain the degree of cooperation which developed between the two originally distinct organisms—the host cell (i. e. the prototypical eukaryote) and bacterial symbiont. It is inconceivable that such cooperation could persist without some form of communication between the respective organisms. That such communication eventually took the form of an exchange of genetic information may be taken for granted. Indeed, research into some of the current symbiotic relationships among microorganisms has found that upon formation of a symbiotic relationship the participating organisms exchange genetic information.[139] And this exchange of information—whether via the agency of RNA, episomes, plasmids, or some other unknown bio-chemical agent—permanently and favorably affects the fate (and genetic heritage) of the respective organisms.

Here there is no denying that this exchange of information between the symbiont and host cell involves nothing less than the inheritance of acquired characters. Waddington conceded this point in a discussion of the hereditary processes operating independently of the chromosomes—via chloroplasts, mitochondria, centrosomes, and the cortex of egg

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[136]*Ibid.*, p. 207. See also J. Darnell, "RNA," *Scientific American* 253: 4 (Oct., 1985), p. 77.

[137]Margulis, *op cit.*, p. 171.

[138]*Ibid.,* p. 183.

[139]*Ibid.*, p. 193.

cells: “Some types of bacterial transformation, or episomal heredity, could even be interpreted as examples of Lamarckian phenomena.”[140]

Stephen Gould indirectly acknowledged the same point in a discussion of viral agents known to infect the genome, albeit in an indirect fashion:

> “I have heard no evidence that any of these biochemical mechanisms leads to the preferential incorporation of *favorable* genetic information. Perhaps this is possible; perhaps it even occurs. If so, it would be an exciting new development, and truly Lamarckian.”[141]

A prime reason for the biologists’ refusal to accept the inheritance of acquired characteristics, in my opinion, can be traced to a general failure to consider the eukaryotic genome from an evolutionary perspective. The genome did not spring into being ready made—like Athena from the head of Zeus. It required many eons to develop and perfect. It stands to reason that during this time the inheritance of acquired characters must have been a driving force in the genome’s evolution.

SEX AND THE SINGLE BACTERIUM

A decisive step in the history of life—yet another which can be traced to our bacterial brethren—occurred when the faculty of sex arose. Bacterial “sex” at first seems to have involved simply the incorporation by one microorganism of a part of another containing several genes. According to Margulis, the number of genes transferred during this process varies—sometimes a few genes, sometimes a large portion of the genome may be transferred.[142] Once again there is no disputing the fact that at the moment this exchange of information first occurred there was an inheritance of acquired characters. And, like the information acquired through the incorporation of bacterial symbionts, the genetic information obtained via this archaeo-sex act was imminently, if not immediately, adaptive in nature.[143]

The incorporation of foreign symbionts, together with the primal sex act, I would suggest, can serve as models for the phylogenetic acquisition of biological information. Thus it is probable that when the first two bacteria succeeded in exchanging genetic information it was largely a matter of chance, and that this exchange, proving useful, became refined through trial and error in the countless generations that followed. Eventually this exchange of genetic information became a routine component of the bacterium’s behavioral repertoire. The ideal model for genome fitness, according to this view, is not the perpetual isolation of the genome—as per the theory of Weismann and Neo-Darwinism—but rather the selective permeability of the genome to information from the

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[140]Waddington, *op cit*., p. 236. The parallel with the Lamarckian view of evolution is made complete inasmuch as there is a delay between the incorporation of the symbionically derived information into the body of the host cell and its eventual transfer to the nuclear genome.

[141]S. Gould, “Shades of Lamarck,” in *The Panda’s Thumb* (New York, 1980), p. 80.

[142]Margulis, *op cit*., p. 27.

[143]Margulis observes that from a functional standpoint the incorporation of symbionts and sexual processes are identical.

outside world, whether understood in the form of neighboring cells or neighboring organisms.

CONCLUSION

A review of the history of evolutionary theory reveals that many of the pioneers in its development were indefatigable supporters of the ancient doctrine of the inheritance of acquired characters. Despite widespread agreement regarding the explanatory power of the Lamarckian theory it was eventually abandoned in the face of the theoretical difficulty of accounting for directional genetic change. Recent developments in bacterial genetics, however, offer compelling evidence that the genome does indeed respond to the needs of the evolving organism. This evidence constitutes *prima facie* evidence for the Lamarckian theory of evolution which, taken in conjunction with the circumstantial evidence derived from paleontology and the study of the behavior of animals, suggests that a return to the ideas of Lamarck and Darwin may soon be in order. At that time and at that time only will a realistic understanding of the evolution of living organisms become possible.