

Lamarck, Evolution, and the Inheritance of Acquired Characters

Richard W. Burkhardt, Jr.¹

Department of History, University of Illinois, Urbana–Champaign, Urbana, Illinois 61801

ABSTRACT Scientists are not always remembered for the ideas they cherished most. In the case of the French biologist Jean-Baptiste Lamarck, his name since the end of the nineteenth century has been tightly linked to the idea of the inheritance of acquired characters. This was indeed an idea that he endorsed, but he did not claim it as his own nor did he give it much thought. He took pride instead in advancing the ideas that (1) nature produced successively all the different forms of life on earth, and (2) environmentally induced behavioral changes lead the way in species change. This article surveys Lamarck's ideas about organic change, identifies several ironies with respect to how his name is commonly remembered, and suggests that some historical justice might be done by using the adjective "Lamarckian" to denote something more (or other) than a belief in the inheritance of acquired characters.

THE French zoologist Jean-Baptiste Lamarck (See Figures 1 and 2) made two important announcements at the Museum of Natural History in Paris on the twenty-seventh day of *floréal*, year 10 of the French Republic (17 May 1802). He made the first in the opening lecture for his course on invertebrate zoology, which met at half past noon. He made the second in a report he gave to his fellow professors later that evening at the Museum's weekly administrative assembly. In his lecture to his students he set forth an unprecedented vision of the gradual, successive production of all the different life forms on earth, from the simplest to the most complex. It was the first comprehensive theory of organic evolution, and it was Lamarck's first extended elaboration of it. In his report to his colleagues he spoke in his capacity as overseer of the Museum's menagerie, a responsibility he had been shouldering since the previous July. He commenced this report with the happy news that the female elephant was completely cured of the digestive problems from she had been suffering.

The first of these two events represents a major, albeit usually neglected, milestone in the history of biology. The second was but a minor episode in the history of the Paris menagerie. At the time, however, the second event drew more attention than did the first. The female elephant's illness had been a cause of considerable anxiety at the Mu-

seum. Live elephants were still a great novelty in Europe at the time, and this particular specimen had the added attraction of being a war trophy, appropriated in 1795 together with a male elephant and other animals from the menagerie of Willem V, the Dutch Stadtholder. Lamarck's colleagues were understandably pleased to learn that the female elephant's health had been restored, especially since the male elephant had died only few months previously. The manuscript *procès-verbal* of the professors' meeting testifies to their satisfaction (Archives Nationales de France, AJ.15.103, p. 57). We have no record, on the other hand, of how Lamarck's students responded to the bold lecture he presented to them earlier in the day. Nor do we have any reason to believe that at the evening meeting Lamarck said anything to his colleagues about what he had just told his students. The irony here is obvious.

It is not unusual to find that an event that looks highly significant in retrospect caused no appreciable stir when it first took place—or at least left no traces of having done so. Lamarck's students may have emerged from his lecture all abuzz, but we do not know that for a fact. If, on the other hand, they were unmoved by the lecture instead of being excited by it, they simply predated in this regard the case of Thomas Bell, the president of the Linnean Society of London, who upon reviewing the Society's meetings for 1858 allowed that nothing capable of revolutionizing science had been brought up in them—despite the fact that he had presided over the meeting of July 1, 1858, where the views of Charles Darwin and Alfred Russel Wallace on natural selection

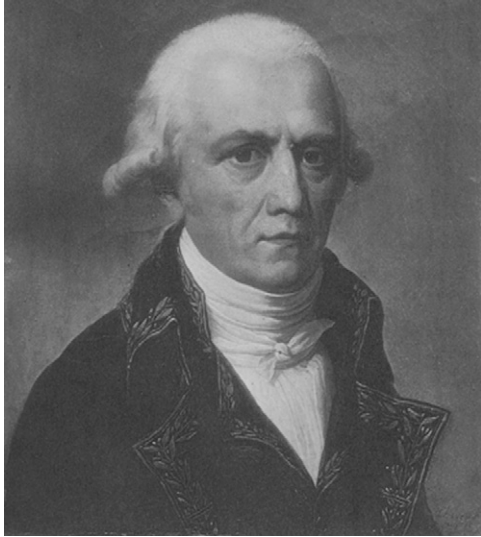


Figure 1 Lamarck in year 10 of the French Republic (1801–1802), wearing the uniform of the Institut de France (from a painting by Thévenin).

received their first public airing (Browne 2002). (For what is known of the students in Lamarck's classes, see Corsi 2001, pp. 329–383.)

In addition to those moments when a historical “turning point” is reached without it being recognized as such, there are the more common cases when the converse is true, *i.e.*, when an event that seems important at the time subsequently drops altogether from historical recollection. When the May 1802 scare regarding the elephant's illness passed, the event seems not to have concerned the professors again, although the animal keepers were surely on the alert never again to allow the elephant to eat an overabundance of fresh grasses. Today, as it happens, Lamarck's name is routinely associated with giraffes (more on this follows), but virtually never with elephants.

With these two variants on the theme of what seems memorable and what does not, over the course of a scientist's career, there is a third that applies with special force in Lamarck's case. This is when someone is remembered for something other than what he or she would have considered to be his or her most significant achievement. Since the end of the nineteenth century, Lamarck's name has been firmly linked with the idea of the inheritance of acquired characters. More recently, “epigenetic inheritance” has been represented as a form of the transmission of acquired characters and thus as a confirmation, at least of a sort, of Lamarck's most famous idea (Gissis and Jablonka 2011). As we show in this article, while it is true that Lamarck endorsed the idea of the inheritance of acquired characters and made use of it in his evolutionary theorizing, neither Lamarck nor his contemporaries treated this as Lamarck's “signature” idea. Certainly he did not claim the idea as his own. Instead, he treated it as commonplace, which it was. He believed it was so transparently obvious that it needed no assemblage of facts or trial by experiment to confirm it.



Figure 2 The statue of Lamarck at the Muséum d'Histoire Naturelle in Paris. The statue was erected in 1909, the centenary of the publication of Lamarck's *Philosophie zoologique* (photo by J. Barrett).

The purpose of this commentary is not to suggest that modern genetic or epigenetic studies constitute a vindication of Lamarck's ideas of two centuries ago. Rather, it is to describe how Lamarck and his contemporaries understood the idea of the inheritance of characters and to see where that idea fit into Lamarck's broader biological theorizing. Nonetheless, it may provide an occasion to reflect briefly on the way that some of the ideas associated with Lamarck's name seem to have renewed appeal.

First, I offer a few very brief notes about Lamarck's scientific career (Landrieu 1909; Corsi 1988; Burkhardt 1977). Lamarck (1744–1829) initially made a scientific name for himself as a botanist attached to the Jardin du Roi (King's Garden) in Paris. When that institution was reconstituted during the French Revolution as the Muséum d'Histoire Naturelle, the new institution's two professorships in botany were given to the botanists René-Louiche Desfontaines (1750–1833) and Antoine-Laurent de Jussieu (1748–1836), and Lamarck was left with the professorship of “insects, worms, and microscopic animals.” In effect, he had the first chair of invertebrate zoology. The little expertise he could claim in this domain was by and large limited to knowledge he had acquired as an avid collector of shells. Like the other professors at the Museum, his job was twofold: (1) to oversee the organization and development of the collections under his charge; and (2) to give an annual course of public lectures on the same area of natural history. He and the 11 other professors of the Museum were also collectively responsible for the Museum's administration.

In the first years that he gave his course, Lamarck offered an introductory lecture wherein he cribbed long passages from the writings of two of his friends, the entomologist G. A. Olivier and the conchologist J.-G. Bruguière (Burkhardt 1977). For his course in 1800, however, he rewrote his introductory lecture completely, and it was there, in the context of discussing the attractions of studying the invertebrates, that he provided what he would later call a “glimpse” of “some important and philosophical views” (Lamarck 1801, p. vi). What was so special about the invertebrates, he told his students at the time, was that these animals showed even better than the vertebrates an “astonishing decrease in complexity of organization” and a “progressive reduction of animal faculties” leading finally to the “least perfect” and “most simply organized” living things—“those perhaps by which nature began, when, with the aid of much time and favorable circumstances, she formed all the others” (Lamarck 1801, pp. 11–12).

How much time did Lamarck have in mind? As he saw it, time, with respect to what nature could accomplish, was essentially unlimited. He never offered a precise estimate of how old he believed the earth might be, but in a work of 1802 he did allow that he was thinking in terms of thousands or even millions of *centuries*. The earth’s age was “so great,” he allowed, “that it is absolutely beyond the power of man to appreciate it in any way” (Lamarck 1802a, p. 7).

As for the different circumstances that nature used to generate all her different productions, these, Lamarck said, were virtually “inexhaustible.” They included “the influence of climates, of variations in the temperature of the atmosphere and all the surrounding environments, of diversities of place, of habits, of movements, of actions, and finally of ways of life, of self-preservation, of self-defense, of multiplication, &c. &c.” As the result of all these influences, Lamarck told his students in 1800, animal faculties are extended and strengthened by use, they become more diverse as animals adopt new habits and maintain them over long periods of time, little by little the parts and organs of the body are likewise affected, and these changes “conserve and propagate themselves by generation” (Lamarck 1801, p. 13). This represented the first time Lamarck called upon the inheritance of acquired characters as a means of accounting for unlimited organic change.

After offering a number of examples of what he had in mind (we return to the question of Lamarck’s examples shortly), Lamarck told his students, “I could prove it is not the form, either of the body or of its parts, that gives rise to habits and way of life of animals, but it is contrary to the habits, the way of life, and all the other influential circumstances that have with time constituted the form of the body and the parts of animals. With new forms, new faculties have been acquired, and little by little nature has arrived at the state where we see it at present” (Lamarck 1801, p. 15).

In this lecture of 1800 Lamarck offered the idea of organic transformation as one of a number of different considerations that made the study of the invertebrates so

significant. In his introductory lecture of 1802, in contrast, he made the idea of the successive development of organic forms the very centerpiece of his remarks. Indeed, he told his students that there was no issue in natural history that was more deserving of their attention (Lamarck 1802b, p. 63). He claimed that life had been successively developed over immense periods of time, beginning with the very simplest forms and proceeding gradually to the most complex. He also offered an explanation, at least in general terms, of how this had been achieved. He maintained that the simplest forms of life had been “directly” generated (others would say “spontaneously” generated) from nonliving matter and that such “direct generations” continued to take place when conditions were favorable. These simple forms became increasingly complex as the result of the hydraulic action of intangible and tangible fluids coursing through them. Direct generation and the constructive action of these moving fluids, abetted by an immense amount of time and an infinite number of diverse and favorable environmental circumstances, were all that nature needed, he said, to bring all the different forms of life into existence.

Where did the inheritance of acquired characters fit into this? In the first place, it entered relatively inconspicuously (though nonetheless critically) into Lamarck’s general explanation of the development of ever-greater organic complexity over time. He allowed that the changes in animal organization produced by the movement of fluids internal to the animal body “were conserved and transmitted successively by generation” (Lamarck 1802b, p. 9). In the second place, and much more conspicuously, it featured in Lamarck’s explanation of the close conformation between an animal’s physical structures on the one hand and its habits or way of life on the other.

Observers since antiquity had recognized what the English naturalist and theologian John Ray subsequently described as “the exact fitness of the parts of the bodies of animals to every one’s nature and manner of living” (Ray 1714, p. 139). What Ray called the “fitness” of parts to purposes, Bishop William Paley a century later would call the “adaptation” of organs to their ends (Paley 1802). For these and other authors of “natural theologies,” everywhere they looked in nature they found testimony to God’s wisdom and goodness in designing the Creation. The most prominent of the French natural theologians of the eighteenth century was the Abbé Pluche, whose *Spectacle de la Nature*, written explicitly for the instruction of young people, was one of the very best selling works in France in the century. In this work, in a dialogue between a count and a countess about birds, Pluche had the count explain to the countess how to understand the great differences in the size and shape of birds’ beaks, necks, legs, and so forth. The count described, for example, how all the features contributing to the heron’s “bizarre” appearance – its long, featherless legs and thighs, its long neck, and its long, sharp, beak, notched at the end – correspond to the way the heron wades in the water and catches the frogs, shellfish, and fish that are its prey (Pluche 1741, pp. 296–297).

Lamarck cited the wading bird example, among others, in setting forth his own understanding of the interrelation of environmental circumstances, needs, habits, and structures. In doing so, he turned the familiar view of the relation between habits and structures on its head. In his lectures of 1800 and 1802 and then later in his *Philosophie zoologique* (*Zoological philosophy*) (Lamarck 1809) he explained how the webbed feet of swimming birds, the curved feet of perching birds, and the long legs of wading birds were all a consequence of their habits, instead of vice versa. In the case of the wading bird he stated: “One perceives that the bird of the shore, which does not at all like to swim, and which however needs to draw near to the water to find there its prey, will be continually exposed to sinking in the mire; but wishing [*voulant*] to behave in such a way that its body does not plunge into the water, it will make its legs contract the habit of extending and elongating themselves. It will result from this for the generations of these birds that continue to live in this manner that the individuals will find themselves elevated as on stilts, on long naked legs . . . ” (Lamarck 1801, p. 14).

In 1802, after providing a host of other examples of this sort (including the development of hooves in herbivores and claws in cats), Lamarck offered the more general statement: “Each change acquired in an organ by a habit of use sufficient to have caused it is then conserved by generation, if it is common to the individuals that in fecundation cooperate together in the reproduction of their species. Finally this change propagates itself and thus passes to all the individuals that follow one another and that are submitted to the same circumstances, without them having been obliged to acquire it by the way that really created it” (Lamarck 1802b, p. 61).

In 1809, in his now famous *Philosophie zoologique*, Lamarck set out this idea more systematically in the form of two laws:

First Law: In every animal that has not reached the end of its development, the more frequent and sustained use of any organ will strengthen this organ little by little, develop it, enlarge it, and give to it a power proportionate to the duration of its use; while the constant disuse of such an organ will insensibly weaken it, deteriorate it, progressively diminish its faculties, and finally cause it to disappear.

Second Law: All that nature has caused individuals to gain or lose by the influence of 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 individuals descending from them, provided that these acquired changes are common to the two sexes or to those which have produced these new individuals (Lamarck 1809, p. 235).

As the historian of science Jean Gayon has properly insisted, despite Lamarck’s clear endorsement of the inher-

itance of acquired characters (as exhibited in Lamarck’s “Second Law”), Lamarck never displayed much interest in the phenomena of heredity as such. What attracted Lamarck’s attention instead was how organisms came to be modified (Gayon 2006). A number of additional points need to be underscored regarding the idea of the inheritance of acquired characters and Lamarck’s endorsement of it.

1. Lamarck presented the idea of the inheritance of acquired characters as self-evident; he never claimed it as his own. In the introduction to his multi-volume *Histoire naturelle des animaux sans vertèbres* (*Natural History of the Invertebrates*), the great work that confirmed his reputation as the founder of invertebrate zoology, Lamarck wrote: “the law of nature by which new individuals receive all that has been acquired in organization during the lifetime of their parents is so true, so striking, so much attested by the facts, that there is no observer who has been unable to convince himself of its reality” (Lamarck 1815, p. 200). It is instructive that the only “experiment” he ever even mentioned in this regard was merely a thought experiment to demonstrate the concept. In 1802 he wrote: “If, with two newborn infants of different sexes one masked their left eyes throughout the course of their lives; if then they [the two individuals] were united together, and one did constantly the same thing with respect to their children, I do not doubt that at the end of a great number of generations, their left eyes would come to disappear naturally and to be gradually obliterated. Following an immense amount of time, the necessary circumstances remaining the same, the right eye would come little by little to shift its position” (Lamarck 1802b, pp. 53–54).

There were many others before Lamarck who endorsed, with greater or lesser certainty, the reality of the inheritance of acquired characters. Notable among these were the naturalist Charles-Georges LeRoy (1723–1789) and the French political philosopher the Marquis de Condorcet (1743–1794). Both of them made reference to the idea in the context of discussing the perfectibility of living things—animals in LeRoy’s case and humans in Condorcet’s. In the posthumous, 1802 edition of Le Roy’s *Lettres philosophiques sur l’intelligence et perfectibilité des animaux* (Le Roy 1802) one finds the following statement by Le Roy with respect to animal instincts: “There is another observation to make on some of the dispositions we consider innate and purely mechanical. It is that they are perhaps absolutely dependent on habits acquired by the ancestors of the individual that we see today. It is proven, by incontestable facts, that a number of dispositions acquired solely through education, when they become habitual and when they have been maintained consecutively in two or three subjects, become almost always hereditary” (Le Roy 1802, pp. 227–228). Similarly Condorcet, writing about the “perfectibility” of humans, suggested that education probably modified and perfected that part of the physical organization of the human body responsible for the mental faculties and that these changes were likely to be among those “individual

perfections” that could be transmitted to successive generations (Condorcet 1794, pp. 383–384). However, such discussions of perfectibility were about changes *within* species. Le Roy, Condorcet, and nearly everyone else at this time who believed in the inheritance of acquired characters were not proposing that the effects of “education” upon habits and/or structures could lead to the creation of new species. As Le Roy put it, “It is impossible that animals, destined by nature for determined ends, and organized accordingly, should not be constrained within circles allocated to their species, in accordance with their needs and means” (Le Roy 1802, p. 224).

2. Lamarck’s innovation with respect to the idea of the inheritance of acquired characters was not in the formulation of the idea as such but instead in his claim—unlike the views of Le Roy and others—that the inheritance of acquired characters was an agent of unlimited change. In brief, although Lamarck did not claim the idea of use inheritance as his own, he did maintain that he was the first to recognize “the importance of this law and the light it sheds on the causes that have led to the astonishing diversity of animals.” He indeed allowed at one point that he put greater stock in having been the first to recognize this law than in the satisfaction he took from “having formed classes, orders, many genera, and a quantity of species in occupying myself with the art of distinctions, an art that constitutes almost the sole object of the studies of other zoologists” (Lamarck 1815, p. 191).
3. Lamarck insisted that specific conditions were necessary for acquired changes to be transmitted to the next generation. As we have seen in Lamarck’s thought experiment with the infants’ eyes and in the “Second Law” of his *Philosophie Zoologique*, he believed that for characters acquired as the result of new habits to be passed via sexual reproduction from one generation to the next, they needed to have been acquired by both parents. When “peculiarities of form or any defects whatever happen to be acquired,” he explained, these changes would be perpetuated only through the union of individuals that had both been changed in the same way. On the other hand, when individuals that had *not* changed in the same way bred with one another, this would “cause all those peculiarities acquired through particular circumstances to disappear” (Lamarck 1809, vol. 1, pp. 261–262). Again in 1815, in his *Histoire naturelle des invertèbres*, he insisted that both parents needed to have undergone the same changes for the inheritance of acquired characters to take place. Here, however, he did allow that if the parents had not been equally modified, a character that had been transformed in one parent might at least be partially transmitted (Lamarck 1815, p. 200).

Would one not expect newly acquired characters to be swamped, as a rule, when the transformed individual was left to breed with individuals that had not undergone the same changes? Lamarck thought otherwise, essentially

supposing that when the individuals of a species were exposed to the *same* new environmental circumstances, they would respond the same way and be modified in the same way. Exposure to new circumstances inevitably happened to organisms all over the world because every place on the earth’s surface was subject, over immense periods of time, to changes of all kinds as climates altered, rivers and ocean beds were displaced, lands were elevated or eroded, and so on. Alternatively, individuals of a species that for one reason or another moved or were transported to new locations and found themselves subject to very different environmental circumstances than those they had previously experienced would take on new forms because of the new habits they acquired and would constitute a new species, distinct from the species remaining in the old location. The new species—and the old one too—would each be constituted by “all the individuals that find themselves in the same situation” (Lamarck 1802b, p. 148).

In addition to the last scenario, Lamarck called attention to the case in which the variation of a particular organic form was continuous over an extended geographic range. He allowed that if one started with a species that one knew well in one’s own country and proceeded to follow it as one traveled farther and farther from home, one could reach the point whereupon comparing the individuals observed last with the individuals observed first, the two sets of individuals appeared to represent two distinct species, even though they would have been connected along the way by a series of varieties. Furthermore, he said, one would not only find “a simple series of varieties, leading from nuance to nuance to the distinct, species,” one would additionally find varieties representing “lateral series, leading to other species still” (Lamarck 1817, pp. 447–448; Burkhardt 1997).

4. Lamarck believed that change was slow and incremental. He also maintained (at least for the most part) that change could be expected only if changed circumstances caused animals to adopt new habits. On the latter score he was not entirely consistent. On the one hand, when he talked about what he called the “power of life,” the sculpting action of fluids in motion, he seems to have represented this as capable of producing the general trend toward increasing complexity irrespectively of the influence of particular environments. On the other hand, when he talked about change at the species level, he insisted that such change took place only when animals took up new habits in response to changed environmental circumstances. The issue was raised in 1802 when Lamarck’s colleague, the zoologist Étienne Geoffroy Saint-Hilaire, returned from Egypt with a collection of mummified specimens of various species. When these specimens were compared with their modern counterparts and it was found that “these animals are perfectly similar to those of today,” this discovery was enlisted as an argument against the notion of organic change, or at least as an indication that over a span of some two or

three thousand years no change had occurred (Lacepède *et al.* 1802; Cuvier 1804). Interestingly enough, Lamarck was one of the cosigners of the Museum of Natural History's report on Geoffroy's collections, but he made clear in subsequent writings that the Egyptian evidence in no way invalidated his views. Insofar as the climate of Egypt had not changed since the time that the specimens in question were embalmed, he said, there was no reason for their descendants to have changed their habits and thus no reason for their forms to have been modified. He remarked caustically of his critics:

I seem to hear those small insects that live for only a year, that inhabit some corner of a building, and that one could suppose occupied with consulting tradition among themselves in order to pronounce on the age of the edifice where they find themselves. Going back twenty-five generations in their meager history, they would decide unanimously that the building that provides their asylum is eternal, or at least that it has always existed, for they have always seen it the same, and they never heard it said that it had a beginning.

The lesson Lamarck wanted his students to draw from this was straightforward: "Great magnitudes, in space and time, are relative." Three to five thousand years, he told the students, was "infinitely small" compared to the time it had taken for the surface of the globe to undergo the great changes to which it had been subjected (Lamarck 1907, p. 541).

That said, Lamarck nonetheless believed that there were examples of organic change that had taken place over the course of human history. All one had to do, he suggested, was to look at wild animals confined to menageries or domesticated animals confined to the barnyard to see the changes produced in them when they were forced to adopt new habits. Similarly, one could compare the form of a French workhorse with that of an English racehorse to see the effect of different habits maintained over many generations. The diverse races of dogs, pigeons, and domesticated plants likewise testified to the changes these forms had undergone in response to the new circumstances to which humans had subjected them (and also, he said, to the mixtures humans produced by interbreeding races developed in different countries) (Lamarck 1907, p. 542).

5. The inheritance of acquired characters was but a tiny item in the broad scheme of Lamarck's theorizing. A sense of the breadth of Lamarck's intellectual ambitions with respect to the whole of biology can be gained from consulting any of the subtitles of his three major treatises on the life sciences (Lamarck 1802b, 1809, 1815). None of them mentions the idea of the inheritance of acquired characters, or, for that matter, even the idea of species

change. One finds reference instead to the broad topics of animal organization, its origin, the cause of its progressive development, and how it comes to be destroyed in the individual (Lamarck 1802b); to diversity of animal organization and the faculties resulting from it, along with the physical causes that maintain life in organized bodies (Lamarck 1809); and to the essential characters of animals, what distinguishes animals from plants and other natural bodies, and "the fundamental principles of zoology" (Lamarck 1815). In the "advertisement" to his *Histoire naturelle des animaux sans vertèbres* in 1815, Lamarck explained that he was offering in the introduction to that work "a truly general theory" concerning "the source of the existence, manner of being, faculties, variations and phenomena of organization of the different animals." Not the least bit bashful about his accomplishment, he claimed this theory to be "linked everywhere in its parts, always consistent in its principles, and applicable to all the known cases" (Lamarck 1815, pp. iii-iv). The theory aimed to elucidate how the simplest forms of life were produced, how animal organization became increasingly complex, how new faculties emerged in conjunction with this increase in organic complexity, and how the influence of particular environmental "circumstances" had given rise to the whole range of diverse habits and structures exhibited in the modern animal world.

Obviously, Lamarck was concerned with much more than change at the species level. Furthermore, his general theory of organic transformation cannot be read simply as an extrapolation from his explanation of change at the species level to change at higher levels. First in 1802, then more systematically in 1809, and once again in 1815, he represented the transformation of organic forms as being the product of two different and opposing factors: (1) the "power of life," responsible for the progressive increase in organic complexity displayed by the different animal classes as one ascended from the simplest polyps at the bottom of the scale to the mammals at the top, and (2) the influence of the environment. The latter was responsible for lateral ramifications from the general linear progression (it was with respect to this level that he offered his observations on how environmentally induced changes in habits and structures led to the transformation of species). Lamarck found it didactically useful to represent these two main factors of organic transformation as operating against each other. It allowed him to offer a quasi-causal explanation of why the most natural ordering of animals (as he saw it) was a general scale of increasing complexity, but one where only the broad animal classes, and not the individual species, could be arranged in a single series. Upon closer inspection, though, one finds that the "power of life" and the influence of the environment were not fundamentally opposed to each other after all. The power of life was nothing other than the creative action of fluids moving first through unorganized and then through organized

bodies, and the subtle fluids (caloric and electricity) that initially gave structure to the simplest life forms emanated from the external environment (Burkhardt 1977). Today Lamarck's identification of life with fluids moving through bodies may seem quaint at best, but it was entirely common throughout the eighteenth century for physicians and physiologists to think about life and health in terms of the interplay of the fluid and solid parts of the body, just as it was common at the end of the eighteenth century and the beginning of the nineteenth century to assume that heat, electricity, and magnetism all depended on the action of specific, subtle, imponderable fluids.

Even with our mention of Lamarck's thoughts on the power of life, however, we are still far from approaching Lamarck's theorizing at its broadest. Over the course of his career he aspired to more than a general theory of the transformation of organic forms from the simplest to the most complex and more than an explanation of the basic phenomenon of life and all its manifestations at the different levels of organic complexity. In his work as a naturalist Lamarck can be appropriately described as first a botanist and then an invertebrate zoologist, but he viewed himself as a "naturalist-philosopher," and in this self-appointed role he was prepared to go well beyond the bounds of the *biologie* of which he aspired to be the founder. As the nineteenth century began, he was planning a grand theoretical enterprise that he characterized as "terrestrial physics." He aimed to provide the theoretical foundations of three related sciences: meteorology (the study of the earth's atmosphere), hydrogeology (the study of the earth's surface and the effects of the movement of waters upon it), and biology (the study of the origin and development of living things) (Lamarck 1802a, pp. 7–8). (See also Corsi 2006.)

Significantly, such confidence in theoretical matters was not new to Lamarck in 1800. Already in the 1790s he had sought to bring his own ideas to bear on chemistry (believing, erroneously, that the new, experimental chemistry of Lavoisier was a step in the wrong direction). The results of his efforts were not positive, either for chemistry or for Lamarck himself. When he read his chemical memoirs at the Institut de France, his colleagues there did their best to ignore him. Rather than doubting his own hypotheses, Lamarck came to believe that there was a conspiracy of silence against him. A discussion of Lamarck's physicochemical theorizing would be out of place in this article. Suffice it to say for our present purposes that by the spring of 1802 Lamarck felt himself at odds with what he took to be the French scientific establishment. He did not expect colleagues who were only interested in what he called "small facts" to welcome the kinds of broader considerations he was presenting to his students. This is one reason why one can suppose with some confidence that on May 17, 1802, after sketching out for his students his broad new theory of organic transformation, he said nothing about this later that day when he met with his fellow professors of the Museum to discuss the administrative matters of the week.

The other reason one can suppose Lamarck did not mention to his colleagues what he had just told his students was that the weekly professorial assemblies at the Museum were devoted to administrative matters, not to discussions of scientific theories or discoveries. The professors were not entirely happy that things had worked out that way, but that is what had transpired (Burkhardt 2007). As for any of his colleagues with whom Lamarck might have offered a quick, confidential report on the lecture he had given earlier in the day, none of the seven professors beside Lamarck who attended the meeting looks like a plausible candidate. The only zoologist there other than Lamarck was the professor of mammals and birds, Etienne Geoffroy Saint-Hilaire (1772–1844), but Geoffroy at this point had only recently returned to Paris after having been away for nearly four years in Egypt and he was actively seeking to reestablish the close friendship he had previously with Georges Cuvier (1769–1832), who in Geoffroy's absence had not only become a major figure in the French scientific community but had also come to take a strong stand against the idea of species transformation. (Cuvier himself was not present at the professorial assembly for the simple reason that he did not yet hold a chair at the Museum. After the death of Jean-Claude Mertrud in October 1802, Cuvier was named professor of animal anatomy.) Of the other professors who were there, Lamarck had no particular reason to expect a favorable reception of his views from André Thouin (agriculture), A.-L. Brongniart (applied chemistry), R.-L. Desfontaines (botany), Gérard Van Spaendonck (painting), or René-Just Haüy (mineralogy). That left Antoine Fourcroy (chemistry), who was certain to be skeptical of Lamarck's style of theorizing given that Lamarck in 1796–1797 had taken Fourcroy's *Philosophie chimique* as the model of the new, experimental pneumatic chemistry that Lamarck wanted to replace with his own, highly speculative, "pyrotic" theory of chemistry (Lamarck 1796).

Although Lamarck may not have hurried to tell his colleagues about his lecture, he was nonetheless eager to get the lecture into print. Originally he thought he would just publish the lecture, bringing it out in short order so that no one could misconstrue or misrepresent anything he had said. Then he decided to expound further on his subject "in order to be better understood." Three months after giving his introductory lecture, he published it as the introduction to his book, *Recherches sur l'organisation des corps vivans* (*Researches on the organization of living bodies*) (Lamarck 1802b). On July 26, 1802 (7 Thermidor year 10 of the Republic) he presented a copy of it to his colleagues. They responded with an official vote of thanks (Archives Nationales de France AJ.15.103, p. 106).

6. Lamarck's thinking has long been characterized (and caricatured) through his examples of the inheritance of acquired characters. Very quickly, it seems, the examples of organic change that Lamarck offered came to characterize his thinking to a degree that was out of proportion to

the importance he attached to them. In addition, careless phrasing by Lamarck led to a common misrepresentation of his thought: the idea that *wishing* or *willing* on an animal's part was a significant factor in Lamarck's account of organic transformation. Of the shorebird, as we have seen, Lamarck wrote, "wishing [voulant] to act in such a way that its body does not plunge into the water, it will make its legs contract the habit of extending and elongating themselves" (Lamarck 1801, p. 14, 1802b, p. 57). However, it is very clear from Lamarck's writings on the relations between animal organization and animal faculties that he denied the capacity of voluntary action to most of the creatures of the animal kingdom. Where others had long defined animals (*vs.* plants) as organisms capable of sensation and voluntary motion, Lamarck insisted that many animals lacked either the first or the second of these, or both. The simplest invertebrates, he said, lacked the capacity of sensation. As for the higher invertebrates, although they possessed sufficiently developed nervous systems to provide them with sensation, their brains were not well enough developed to allow them the capacity for thought and volition. It was only in the vertebrates, and primarily in the birds and the mammals, that brain development made this possible, but even among the birds and mammals—and indeed even in humans, Lamarck said most actions took place as a result of habit without thought or volition being involved (Lamarck 1809, vol. 2, pp. 336–338; Burkhardt 2011).

After Lamarck's death, Georges Cuvier wrote the "eulogy" to be delivered for Lamarck at the Académie des Sciences. Using the occasion to offer an object lesson in how *not* to do science, Cuvier mocked Lamarck's various speculative enterprises. He also called specific attention to Lamarck's statements about the swimming bird, the shore bird, and so on, citing Lamarck's own words to support the claim that Lamarck believed "that desires, efforts, can engender organs" (Cuvier 1834, pp. 199–200). Lamarck, admittedly, had left himself open to this charge and to the jests that Cuvier was happy to make about him (Burkhardt 1977). There were serious scientific objections Cuvier could have made to the idea of species transformation, but he preferred not to give Lamarck's transformist ideas scientific credibility by treating them seriously (Coleman 1964; Burkhardt 1977).

As for Lamarck's giraffe example, the prominence of this example in the historic recollection of Lamarck stands in striking contrast to the inconsequential manner in which he first introduced it. His first mention of the case of the giraffe appeared in his 1802 book, *Researches on the Organization of Living Bodies*. It appeared furthermore as an afterthought, not in the text but instead in the *index* to the book. Under the heading "habitudes des animaux" (animal habits) he included the observation: "To the examples I have cited I would be able to add that of the form of the giraffe (camelopardalis), herbivorous animal that, living in the places where the land is arid and without herbage, finds itself

obliged to browse the leaves of the trees and to strive continually to reach there" (Lamarck 1802b, p. 208). Seven years later, in his *Philosophie zoologique*, Lamarck elaborated on the example and promoted it to a position in his main text, writing:

In regard to habits, it is interesting to observe a product of them in the particular form and height of the giraffe (camelo-pardalis). This animal, the largest of the mammals, is known to live in the interior of Africa in places where the earth is nearly always arid and without herbage, obliging it to browse on the leaves of trees and to continually strive to reach up to them. It has resulted from this habit, maintained for a long time by all the individuals of the race, that the forelegs have become longer than the hind legs and its neck has so lengthened itself that the giraffe, without standing on its hind legs, raises its head and reaches a height of six meters (nearly twenty feet) (Lamarck 1809, vol. 1, pp. 256–257).

7. Lamarck's examples and his model of species change were about *functional*, adaptive changes. This was also true for at least some of his thinking about the evolution of higher taxa. This model was a simple one: animals adopt new habits in response to changes in the conditions surrounding them, such changes in habits lead to changes in structures, and the new habits and new structures are passed on to succeeding generations, accumulating to the point of producing new species. Habit change, he suggested in his *Philosophie zoologique*, was also responsible for the origins of certain of the higher animal taxa. His observations on a live seal brought to the Museum of Natural History at the end of June 1809 were the occasion for him to append some last-minute "additions" to his *Philosophie zoologique* before it appeared in print (in August 1809). These related specifically to the chapters in the first volume of the work on (1) the influence of the environment on animal habits and structures and (2) how to represent the natural order of animals. Lamarck watched how the seal moved in the water and on the land, noting in particular how it used its hind legs and forelegs. He observed that the seal put its hind legs together as a fin when swimming but kept these legs separate for finer manipulations when seizing its prey. He compared this with the walrus, where the hind legs, he said, are usually physically united in a caudal fin. He explained that the seal's habit of eating fish and other marine prey *vs.* the walrus's habit of eating plants had led to the difference in the conformation of their hind legs, which provided "a new proof of the power of habit over the form and state of organs."

After offering some other examples of the power of habit, Lamarck then remarked on which classes of animals had given rise to which other classes of animals, and he speculated at some length on the origin of the mammals. The mammals, he maintained, came from one of two branches of the reptiles (the other branch leading to the birds). The "saurian" branch

of the reptiles, he said, gave rise to “those aquatic mammals we call amphibians.” The diverse habits taken up by these creatures then led to the cetacean mammals (which returned to the sea and came up to the surface of the water only to breathe) and two forms of terrestrial mammals: the ungulates (those with hooves) and the unguiculates (those with nails or claws). He suggested that plant-eating amphibian mammals like walruses and manatees had given rise to the ungulates, while the fish-eating amphibian mammals like seals had given rise to the terrestrial carnivores (Lamarck 1809, vol. 2, pp. 451–466).

Lamarck allowed that while these arguments would “only seem to be simple conjectures,” he felt that closer consideration of his arguments and of the habits and environments of the animals he had cited would show that his suggestions had “a probability of the highest degree” (Lamarck 1809, vol. 2, p. 462). High probability or not, these comments indicate how central habit and environment were to his thinking about organic change not only at the species level but above it.

8. Lamarck offered no explanation of the mechanisms by which acquired characters were transmitted from one generation to the next. This is in no way surprising, given that in his day the scientific study of variation and heredity was yet to be envisioned (see Müller-Wille and Rheinberger 2007; Müller-Wille and Rheinberger 2012). Lamarck wrote his *Philosophie zoologique* three decades before the beginnings of cell theory, half a century before the work of Mendel (the importance of which was not recognized until 1900), and more than 60 years before fertilization was shown to involve the union of one sperm and one egg. Lamarck did have some things to say about generation, but what he said suggests how far he was from thinking about specific ways to account for the transmission of acquired characters, given that generation for him was essentially a question of transmitting vital motion. As he explained sexual reproduction, fertilization involved an “invisible flame or subtle vapor” emanating from the “fertilizing matter,” insinuating itself in the “gelatinous molecule susceptible of fecundation,” and through its “expansive motion” bringing order and vital movement to the tiny body on which it operated. He acknowledged that the subtle, fertilizing fluid would have to be able to be species specific—it would have to have “undergone a particular modification in each species, either through mixtures or combinations, or in another way”—but aside from this he had nothing to offer. The process of fecundation, he admitted, remained an “admirable mystery.” He was very keen to suggest, on the other hand, that what happened in fertilization through the action of the subtle fertilizing fluid was paralleled by how nature brought life “directly” to minute, unorganized bodies of gelatinous or mucilaginous matter when the conditions were right, through the action of the subtle fluid of heat (perhaps aided by the subtle fluid of

electricity) (see Lamarck 1802b, pp. 95–98; 1809, vol. 2, pp. 70–90).

9. Lamarck himself never used the phrase “the inheritance of acquired characters,” nor for that matter did he ever use the words “heredity” or “hereditary.” There was, however, a contemporary of Lamarck’s at the Museum of Natural History in Paris who used the words “heredity” and “hereditary” and who endorsed the concept that acquired modifications could become hereditary, but who denied that this process could go far enough to produce species change (Gayon 2006; Burkhardt 2011). This was the zoologist Frédéric Cuvier, the younger brother of Georges Cuvier, Lamarck’s great opponent on the subject of evolution. Put in charge of the Museum of Natural History’s menagerie late in 1803, Frédéric Cuvier set about trying to build a scientific career based primarily on the study of living animals. Gayon has identified an 1811 article by Frédéric Cuvier on different dog breeds as the first time that the word “*héréditaire*” (hereditary) was used in French with respect to the transmission of acquired modifications, rather than in the medical context of hereditary diseases, where the word *héréditaire* had already been in use for some time. In fact one finds the word hereditary used with respect to the transmission of acquired variations as early as the 1802 edition of Le Roy’s *Lettres philosophiques sur l’intelligence et la perfectibilité des animaux* (cited above), while Cuvier used the word as early as 1807 (Cuvier 1807). In the following year, offering observations on the mental faculties of animals, Cuvier maintained “that some of the qualities that are regarded as belonging to instinct in animals are subject to the same laws as those that depend on education.” Qualities that are acquired through education, he allowed, “become finally instinctive or hereditary as soon as they have been exercised over a series of sufficient generations.” In contrast, “they become obliterated or wear away more or less, after their exercise ceases to fortify or sustain them” (Cuvier 1808, p. 462; Burkhardt 2011). Strikingly, Cuvier made no mention of Lamarck in this regard. Instead he credited the idea of the transmission of acquired modifications to Leroy.

The word heredity seems to have appeared for the first time in a biological context (as opposed to the legal context in which it was already used) in a report on an article Frédéric Cuvier gave at the Société philomathique in 1812 (Cuvier 1812). The report states that Cuvier presented in his article the “rule” or “law” that “acquired faculties propagate themselves by generation and become hereditary.” The report goes on to say that Cuvier used this rule to discuss “the cause of the existence of races and what they owe to this heredity.” [Gayon gives a much later date for the first appearance of the word “heredity”—1841—but in that case too the reference, made by Pierre Flourens, was to Frédéric Cuvier’s work (Gayon 2006).]

Frédéric Cuvier clearly was an exponent of the idea that came to be called the inheritance of acquired characters. He cited modifications produced by use or disuse (together with what he called “accidental modifications” chosen by animal breeders) as the basis for the formation of races of domestic animals. However, he also quite clearly denied that such changes could go far enough to produce new species. They could not be used, he said, “in support of the systems by which one has wanted to deduce the different forms of animals from the diverse circumstances which have been able to influence them” (Cuvier 1811, p. 353; Burkhardt 2011).

Lamarck died in 1829. Georges Cuvier died three years later. Georges Cuvier had done his best to dampen any enthusiasm for transformist thinking, but a number of naturalists were nonetheless attracted to it, even if they had not endorsed or developed the idea in as comprehensive, systematic, or forthright a fashion as Lamarck had done (Corsi 1988). In 1834, Frédéric Cuvier, writing the introduction for the fourth edition of his brother’s *Recherches sur les ossements fossils (Researches on Fossil Bones)*, felt the need to defend his brother’s reputation and to deny any truth of recent ideas of species change. He indicated that there were no observational or experimental grounds for endorsing the transformist notions of Buffon, Lamarck, or any more recent writers. Then, in a statement that makes one think ahead to Thomas Bell pointedly ignoring the revolutionary nature of the ideas of Darwin and Wallace, the younger Cuvier wrote: “Ah! If there existed the feeblest proof, I would say not even of the transformation, but of the possibility of the transformation of one species into another species, how would it be possible for an anatomist, a physiologist, or a naturalist to be able to direct his attention thereafter to any other sort of phenomena?” One would have to have not reflected on all that was miraculous about such a transformation, Cuvier suggested, “to believe that at the very instant when it was recognized to be possible, it would not produce a fundamental revolution in all the sciences that have animals to a greater or lesser degree as their subject” (Cuvier 1834, vol. 1, p. xxii; Burkhardt 2011).

One recognizes in retrospect that what Frédéric Cuvier could not imagine happening did indeed happen, even if took more than an “instant” for the revolution in the life sciences to occur. This revolution is most commonly known as the “Darwinian revolution.” We misrepresent the development of biological thought, however, if we simply view this revolution through the familiar lens that contrasts Darwinian natural selection on the one hand with the “Lamarckian” idea of the inheritance of acquired characters on the other.

10. The fact is that Darwin himself was a firm believer in the inheritance of acquired characters. In his *On the Origin of Species* he identified the inheritance of acquired characters as one of the sources of variation on which natural selection acts (Darwin 1859). Nine years later in his *Variation of Animals and Plants Under Domestication*,

Darwin offered his “provisional hypothesis of pangenesis” to account for a whole range of phenomena related to heredity and development, including the inheritance of acquired characters (Darwin 1868). In 1880, two years before his death, responding to a critique by Sir Wyville Thomson, Darwin rejected the assertion that his theory of species change depended only on natural selection. He referred back to his work of 1868 saying, “I believe that no one has brought forward so many observations on the effects of use and disuse of parts, as I have done, in my *Variation of Animals and Plants Under Domestication*” (Darwin 1880).

Darwin had indeed paid considerable attention to the effects of use and disuse of parts (among other things), in his big, two-volume work on variation. In his “provisional hypothesis of pangenesis,” he postulated that small, material particles that he called “gemmules” were produced in all the cells of the body, subsequently collected in the gonads and transmitted in reproduction, and accounted for a remarkable battery of hereditary and developmental phenomena, including (among others) reversion, “prepotency,” “the influence of the male element on the female form,” organs developed in the wrong place, the regeneration of lost parts, the direct action of changed conditions, and “the inherited effects of the use or disuse of particular organs.” With respect to the last two of these Darwin wrote,

On any ordinary view it is unintelligible how changed conditions, whether acting on the embryo, the young or adult animal, can cause inherited modifications. It is equally or even more unintelligible on any ordinary view, how the effects of the long-continued use or disuse of any part, or of changed habits of body or mind, can be inherited. A more perplexing problem can hardly be proposed; but on our view we have only to suppose that certain cells become at last not only functionally but structurally modified; and that these throw of similarly modified gemmules” (Darwin 1868, vol. 2, p. 395).

Reiterating this he stated,

In the cases in which the organization has been modified by changed conditions, the increased use or disuse of parts, or any other cause, the gemmules cast off from the modified units of the body will be themselves modified, and, when sufficiently multiplied, will be developed into new and changed structures” (Darwin 1868, vol. 2, p. 395).

Lamarck, in contrast, as we have seen, had not offered any particular hypothesis about how acquired characters might be transmitted from one generation to the next. His focus was on the changes that individuals underwent as the result of adopting new habits. His emphasis, in other words, was on the use and disuse side of the equation (law 1 of his *Philosophie zoologique*), not the hereditary transmission side of it (law 2). He did not identify a range of different hereditary phenomena in need of explanation. He made a few references to changes being lost in sexual reproduction if both parents had not undergone the same changes, but he did not worry about other hereditary phenomena such as

reversion. As indicated above, the very notion of a science of heredity had not yet begun to take shape in his day.

Here then is another reason to qualify both the common association of Lamarck's name with the idea of the inheritance of acquired characters and the equally familiar contrast between Lamarck's idea of the inheritance of acquired characters with Darwin's idea of natural selection. It was Darwin, not Lamarck, who offered a theory to explain how characters acquired as the result of use and disuse were transmitted from one generation to the next. It was also Darwin, as we have seen, who allowed that he had provided more evidence on the effects of use and disuse than anyone before him. Curiously enough, to add another historical irony (or perhaps even indignity) when it comes to Lamarck and the idea of the inheritance of acquired characters, in the whole of Darwin's *Variation of Animals and Plants under Domestication*, where Darwin offered his many examples of the effects of use and disuse, he never once mentioned Lamarck's name. It might be said that Darwin outdid Lamarck at what is typically taken to have been Lamarck's own game but never acknowledged Lamarck in the process.

What we have said thus far does not exhaust all the historical ironies with respect to the various ways Lamarck's name has figured in discussions of how evolution works. We will leave aside here the decades immediately after Darwin's death, when August Weismann launched his assault on the idea of the inheritance of acquired characters and vigorous debates between self-styled "neo-Darwinians" on the one hand and "neo-Lamarckians" on the other, and turn to the beginning of the twentieth century to consider yet another historical twist in which Lamarck's name was part of the package. In the early years of the twentieth century, neo-Darwinians and neo-Lamarckians were not the only rival theorists in the effort to identify the mechanisms by which evolution takes place. Among the other theories in vogue at the time—and one that furthermore held special appeal for experimental biologists—was the "mutation theory" of Hugo de Vries (de Vries 1901; Allen 1975). As it happened, there was one single species that featured in de Vries' theory that new species could arise in a single generation as the result of but a single large jump or mutation. This species was the evening primrose, a plant named *Oenothera lamarckiana* after the French biologist. Lamarck had called it *Aenothera grandiflora* when he described it in the 1790s, but the plant was renamed in Lamarck's honor by N. C. Seringe in 1828 (see Davis 1912). The irony here is that a plant named after Lamarck ended up starring in a particular explanation of species change that could scarcely have been more un-Lamarckian. The abrupt, discrete, discontinuous mutations featured in de Vries's theory bore no resemblance to the slow, virtually imperceptible, continuous changes of Lamarck's evolutionary hypothesizing.

Recently Lamarck's name has undergone something of a revival. Gissis and Jablonka, in a conference volume entitled *Transformations of Lamarckism*, promoted the view that at least certain kinds of modern work on developmental

plasticity, epigenetic inheritance, and biological individuality can be properly construed as representative of a "Lamarckian problematic," characterized by a "developmental-variation first' approach to evolutionary problems" (Gissis and Jablonka 2011, p. 145). They take care to assert, however, that "endorsing 'Lamarckian problematic' does not entail commitment to Lamarck's specific (and sometimes inconsistent) views, nor to the views of later Lamarckians" (Gissis and Jablonka 2011, p. 154).

This leaves one to ask, however, What are the parts of Lamarck's original thinking that one might want to highlight and perhaps even to preserve in some suitably modern form? How far can we transform the transformist without doing a disservice to how we understand him in his own time? This author (who began his career as a historian of biology studying Lamarck) would certainly not be discontent if every time Lamarck's name were mentioned one did not have to suppose that one was talking about the inheritance of acquired characters. As we have seen, Lamarck clearly endorsed the idea, and it served as a necessary part of his theorizing, but he never saw it as an issue, nor did his contemporaries seem to take it as one. In contrast, Lamarck did take pride in promoting the idea of the successive production of living forms, beginning from the very simplest of all living things and proceeding gradually up to the most complex. His discussions of the links between the different levels of animals organization and the faculties enjoyed by the animals at those levels may seem much too primitive or vague to provide any inspiration for scientists today, but we should at least remember that these issues counted very much for him. He sought a causal explanation of the growth of organic complexity and he likewise sought to understand how different faculties arose in conjunction with that complexity.

As for Lamarck's thoughts on change at the species level, Lamarck deserves to be remembered for having emphasized the role of behavior in the evolutionary process. From the moment of his first announcement of his new ideas on organic mutability onward, this idea was essential to his thinking. To recite his claim of 1800:

I could prove it is not the form, either of the body or of its parts, that gives rise to habits and way of life of animals, but it is to contrary the habits, the way of life, and all the other influential circumstances that have with time constituted the form of the body and the parts of animals.

Would a renewed attention to behavior as a factor in evolution deserve to be called "Lamarckian"? Surely it would depend on how it was framed. When it comes to thinking about the role of behavior in animal evolution, there may have been no more eloquent discussion offered in the last 50 years than that provided 50 years ago by Alister Hardy in his Gifford Lectures of 1963. In the volume of lectures subsequently published as *The Living Stream* (Hardy 1965), Hardy made it abundantly clear that he was a Darwinian and a Mendelian. He happily acknowledged, furthermore, that there were many examples of adaptation

that could not be explained by any Lamarckian principle. He had no trouble denying the inheritance of acquired characters. Nonetheless he did believe that via the “Baldwin effect” or “organic selection” (which he likened to Waddington’s “genetic assimilation”), behavioral initiatives in the form of changes of habit had an important role to play in animal evolution, at least at the level of the birds and mammals. As he saw it, advantageous changes of habit could spread in a population via imitation or learning, *i.e.*, nongenetically, and pave the way for the selection of any genetic changes that happened to make the new habits more effective. Wrote Hardy of the beak shapes of Darwin’s finches as described by David Lack, “What is the more reasonable explanation of these adaptations: that chance mutations, first occurring in a few members of the population, caused these birds to alter their habits and seek new food supplies more suitable to their beaks and so become a more successful and surviving race, or did the birds, forced by competition, adopt new feeding habits which spread in the population so that chance changes in beak form giving greater efficiency came gradually to be preserved by organic selection?” (Hardy 1965, pp. 174–175).

Hardy’s idea that behavioral change can be a driving force in organismal evolution has not gone unnoticed by geneticists studying avian evolution. To explain “the high rate of anatomical evolution in birds and the especially high rate in songbirds,” Wyles *et al.* (1983)—with specific reference to Hardy’s hypothesis (but without mentioning the name of Lamarck)—have identified the acquisition and spread of new habits as critical initiators of evolutionary change among certain higher animals. They propose that behavioral innovation and social transmission lead to new selection pressures that then favor “those mutations that improve the individual’s effectiveness at living in the new way.” The authors suggest that this hypothesis would explain not only the high rates of anatomic evolution in songbirds but also in the higher primates and especially the genus *Homo*.

This article began with comments on various ways that scientists are remembered (or not) for particular ideas. Lamarck has come to be remembered primarily for the idea of the inheritance of acquired characters, an idea in which he invested no intellectual energy and for which he never expected or cared to be remembered. In contrast, the ideas for which he would have wanted to be remembered (relative to the topic of organic mutability) were his broad view of the successive production of all living forms from the simplest to the most complex and his idea that behavioral change was a leading factor in organismal change. Could we manage to change the common meaning of the adjective “Lamarckian”? Might we allow that Hardy’s views or comparable thoughts on behavioral evolution embody a certain “Lamarckian insight,” even if they involve accounts where Darwinian natural selection has a deciding role with respect to what survives and what does not? Might we shed the long-term habit of linking Lamarck’s name so exclusively with the idea of the inheritance of acquired characters?

Lamarck recognized the difficulty of changing long-maintained habits, but he also recognized that in new environments new habits have a chance to take root. Perhaps new work in genetics, development, and evolution will make it possible to provide the adjective “Lamarckian” with new meaning.

Literature Cited

- Allen, G. E., 1975 *Life Science in the Twentieth Century*. Wiley, New York.
- Archives Nationales de France Procès verbaux des assemblées des professeurs. Fonds Muséum d’Histoire Naturelle. AJ.15.103, 1801–1802 (Manuscript minutes of the meetings of the Professors of the Muséum d’Histoire Naturelle from 17 Pluiose an 10 to 1 Frimaire an 11 [6 February 1801 to 22 November 1802]).
- Browne, J., 2002 *Charles Darwin: The Power of Place*. Jonathan Cape, London.
- Burkhardt, Jr., R. W., 1977 *The Spirit of System: Lamarck and Evolutionary Biology*. Harvard University Press, Cambridge, MA/London.
- Burkhardt, Jr., R. W., 1997 Unpacking Baudin: models of scientific practice in the age of Lamarck, pp. 497–514 in *Jean-Baptiste Lamarck, 1744–1829*, edited by G. Laurent. Éditions du CTHS, Paris.
- Burkhardt, R. W. Jr., 2007 The Leopard in the garden: life in close quarters at the Muséum d’Histoire Naturelle. *Isis* 98: 675–694.
- Burkhardt, Jr., R. W., 2011 Lamarck, Cuvier, and Darwin on animal behavior, pp. 33–44 in *Transformations of Lamarckism: From Subtle Fluids to Molecular Biology*, edited by S. B. Gissis and E. Jablonka. MIT Press, Cambridge, MA/London.
- Coleman, W., 1964 *Georges Cuvier, Zoologist: A Study in the History of Evolution Theory*. Harvard University Press, Cambridge, MA.
- Condorcet, J.-A.-N. de C., 1794 *Esquisse d’un tableau historique des progrès de l’esprit humain: Ouvrage posthume de Condorcet*. Agasse, Paris.
- Corsi, P., 1988 *The Age of Lamarck: Evolutionary Theories in France, 1790–1830*. University of California Press, Berkeley.
- Corsi, P., 2001 *Lamarck. Genèse et enjeux du transformisme, 1770–1830*. CNRS Éditions, Paris.
- Corsi, P., 2006 Biologie, pp. 37–64 in *Lamarck, Philosophe de la Nature*, edited by P. Corsi, J. Gayon, G. Gohau, and S. Tirard. Presses Universitaires de France, Paris.
- Cuvier, F., 1807 Du rut. *Ann. Must. Hist. Nat.* 9: 118–130.
- Cuvier, F., 1808 Observations sur le chien des habitans de la Nouvelle-Hollande, précédés de quelques réflexions sur les facultés morales des animaux. *Ann. Mus. Hist. Nat.* 11: 458–476.
- Cuvier, F., 1811 Recherches sur les caractères ostéologiques qui distinguent les principales races du chien domestique. *Ann. Mus. Hist. Nat.* 18: 333–353.
- Cuvier, F., 1812 Essais sur les facultés intellectuelles des brutes. *Nouv. Bull. Sci. Soc. Philomat.* 3: 217–218.
- Cuvier, F., 1834 Observations préliminaires, pp. i–xxiv in *Recherches sur les ossemens fossiles*, by G. Cuvier, ed. 4, vol. 1. E. d’Ocagne, Paris.
- Cuvier, G., 1804 Mémoire sur l’ibis des anciens Égyptiens. *Ann. Mus. Hist. Nat.* 4: 116–135.
- Darwin, C., 1859 *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. John Murray, London.
- Darwin, C., 1868 *The Variation of Animals and Plants under Domestication*. John Murray, London.
- Darwin, C., 1880 Sir Wyville Thomson and natural selection *Nature* 23: 32.

- Davis, B. M., 1912 Was Lamarck's evening primrose (*Oenothera lamarckiana* Seringe) a form of *Oenothera grandiflora* Solander? *Bull. Torrey Bot. Club* 39: 519–533.
- de Vries, H., 1901 *Die Mutationstheorie. Versuche und Beobachtungen über die Entstehung von Arten im Pflanzenreich*. Veit, Leipzig.
- Gayon, J., 2006 Hérité des caractères acquis, pp. 105–163 in *Lamarck, Philosophe de la Nature*, edited by P. Corsi, J. Gayon, G. Gohau, and S. Tirard. Presses Universitaires de France, Paris.
- Gissis, S., and E. Jablonka, 2011 *Transformations of Lamarckism: From Subtle Fluids to Molecular Biology*. MIT Press, Cambridge, MA/London.
- Hardy, A. S., 1965 *The Living Stream*. Harper & Row, New York/Evanston, IL.
- Lacépède, B. G. E., G. Cuvier, and J.-B. Lamarck, 1802 Rapport des professeurs du Muséum, sur les collections d'histoire naturelle rapportées d'Égypte, par E. Geoffroy. *Ann. Mus. Hist. Nat.* 1: 234–241.
- Lamarck, J.-B., 1796 *Réfutation de la théorie pneumatique ou de la nouvelle doctrine des chimistes modernes*. Agasse, Paris.
- Lamarck, J.-B., 1801 *Système des animaux sans vertèbres... ; précédé du Discours d'ouverture de l'an VIII de la République*. Déterville, Paris.
- Lamarck, J.-B., 1802a *Hydrogéologie, ou Recherches sur l'influence qu'ont les eaux sur la surface du globe terrestre; sur les causes de l'existence du bassin des mers, de son déplacement et de son transport successif sur les différens points de la surface du globe: enfin sur les changemens que les corps vivans exercent sur la nature et l'état de cette surface*. Agasse et Maillard, Paris.
- Lamarck, J.-B., 1802b *Recherches sur l'organisation des corps vivans et particulièrement sur son origine, sur la cause de ses développemens et des progrès de sa composition, et sur celle qui, tendant continuellement à la détruire dans chaque individu, amène nécessairement sa mort; précédé du discours d'ouverture du cours de zoologie, donné dans le Muséum national d'Histoire Naturelle*. Maillard, Paris.
- Lamarck, J.-B., 1809 *Philosophie zoologique, ou exposition des considérations relatives à l'histoire naturelle des animaux; à la diversité de leur organisation et des facultés qu'ils en obtiennent; aux causes physiques qui maintiennent en eux la vie et donnent lieu aux mouvemens qu'ils exécutent; enfin, à celles qui produisent les unes le sentiment, et les autres l'intelligence de ceux qui en sont doués*. Baillièrre, Paris.
- Lamarck, J.-B., 1815 *Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; précédée d'une introduction offrant la détermination des caractères essentiels de l'animal, sa distinction du végétal et des autres corps naturels; enfin, l'exposition des principes fondamentaux de la zoologie*, vol. 1. Déterville, Paris.
- Lamarck, J.-B., 1817 Espèce. *Nouveau Dictionnaire d'Histoire Naturelle* 10: 441–451.
- Lamarck, J.-B., 1907 Discours d'ouverture d'un cours de zoologie, prononcé en prairial an XI, au Muséum d'Histoire naturelle, sur la question: Qu'est-ce que l'espèce parmi les corps vivans? *Bull. Sci. Fr. Belg.* 40: 523–543.
- Landrieu, M., 1909 *Lamarck, le fondateur du transformisme: Sa vie, son œuvre*. Société zoologique de France, Paris.
- Le Roy, C.-G., 1802 *Lettres philosophiques sur l'intelligence et la perfectibilité des animaux, avec quelques lettres sur l'homme*. Boscange, Masson et Besson, Paris.
- Müller-Wille, S., and H.-J. Rheinberger, eds., 2007 *Heredity Produced: At the Crossroads of Biology, Politics, and Culture, 1500–1870*. MIT Press, Cambridge, MA/London.
- Müller-Wille, S., and H.-J. Rheinberger, 2012 *A Cultural History of Heredity*. University of Chicago Press, Chicago/London.
- Paley, W., 1802 *Natural Theology; or, Evidences of the Existence and Attributes of the Deity*. Robert Faulder, London.
- Pluche, N.-A., 1741 *Spectacle de la nature, ou Entretiens sur les particularités de l'histoire naturelle, qui ont paru les plus propres à rendre les jeunes gens curieux et à leur former l'esprit*. Compagnie des Libraires, Amsterdam.
- Ray, J., 1714 *The Wisdom of God Manifested in the Works of Creation*. Ed. 6. William Innys, London.
- Wyles, J. S., J. G. Kunkel, and A. C. Wilson, 1983 Birds, behavior and anatomical evolution. *Proc. Natl. Acad. Sci. USA* 80: 4394–4397.

Communicating editor: A. S. Wilkins