7 | Shades of Lamarck

THE WORLD, UNFORTUNATELY, rarely matches our hopes and consistently refuses to behave in a reasonable manner. The psalmist did not distinguish himself as an acute observer when he wrote: "I have been young, and now am old; yet have I not seen the righteous forsaken, nor his seed begging bread." The tyranny of what seems reasonable often impedes science. Who before Einstein would have believed that the mass and aging of an object could be affected by its velocity near the speed of light?

Since the living world is a product of evolution, why not suppose that it arose in the simplest and most direct way? Why not argue that organisms improve themselves by their own efforts and pass these advantages to their offspring in the form of altered genes—a process that has long been called, in technical parlance, the "inheritance of acquired characters." This idea appeals to common sense not only for its simplicity but perhaps even more for its happy implication that evolution travels an inherently progressive path, propelled by the hard work of organisms themselves. But, as we all must die, and as we do not inhabit the central body of a restricted universe, so the inheritance of acquired characters represents another human hope scorned by nature.

The inheritance of acquired characters usually goes by the shorter, although historically inaccurate, name of Lamarckism. Jean Baptiste Lamarck (1744-1829), the great French biologist and early evolutionist, believed in the inheritance of acquired characters, but it was not the centerpiece of his evolutionary theory and was certainly not original with him. Entire volumes have been written to trace its pre-Lamarckian pedigree (see Zirkle in bibliography). Lamarck argued that life is generated, continuously and spontaneously, in very simple form. It then climbs a ladder of complexity, motivated by a "force that tends incessantly to complicate organization." This force operates through the creative response of organisms to "felt needs." But life cannot be organized as a ladder because the upward path is often diverted by requirements of local environments; thus, giraffes acquire long necks and wading birds webbed feet, while moles and cave fishes lose their eyes. Inheritance of acquired characters does play an important part in this scheme, but not the central role. It is the mechanism for assuring that offspring benefit from their parents' efforts, but it does not propel evolution up the ladder.

In the late nineteenth century, many evolutionists sought an alternative to Darwin's theory of natural selection. They reread Lamarck, cast aside the guts of it (continuous generation and complicating forces), and elevated one aspect of the mechanics—inheritance of acquired characters—to a central focus it never had for Lamarck himself. Moreover, many of these self-styled "neo-Lamarckians" abandoned Lamarck's cardinal idea that evolution is an active, creative response by organisms to their felt needs. They preserved the inheritance of acquired characters but viewed the acquisitions as direct impositions by impressing environments upon passive organisms.

Although I will bow to contemporary usage and define Lamarckism as the notion that organisms evolve by acquiring adaptive characters and passing them on to offspring in the form of altered genetic information, I do wish to record how poorly this name honors a very fine scientist who died 150 years ago. Subtlety and richness are so often degraded in our world. Consider the poor marshmallow—the plant, that is. Its roots once made a fine candy; now its name

adheres to that miserable ersatz of sugar, gelatine, and corn

Lamarckism, in this sense, remained a popular evolutionary theory well into our century. Darwin won the battle for evolution as a fact, but his theory for its mechanism—natural selection-did not win wide popularity until the traditions of natural history and Mendelian genetics were fused during the 1930s. Moreover, Darwin himself did not deny Lamarckism, although he regarded it as subsidiary to natural selection as an evolutionary mechanism. As late as 1938, for example, Harvard paleontologist Percy Raymond, writing (I suspect) at the very desk I am now using, said of his colleagues: "Probably most are Lamarckians of some shade; to the uncharitable critic it might seem that many out-Lamarck Lamarck." We must recognize the continuing influence of Lamarckism in order to understand much social theory of the recent past-ideas that become incomprehensible if forced into the Darwinian framework we often assume for them. When reformers spoke of the "taint" of poverty, alcoholism, or criminality, they usually thought in quite literal terms—the sins of the father would extend in hard heredity far beyond the third generation. When Lysenko began to advocate Lamarckian cures for the ills of Soviet agriculture during the 1930s, he had not resuscitated a bit of early nineteenth-century nonsense, but a still respectable, if fast fading, theory. Although this tidbit of historical information does not make his hegemony, or the methods he used to retain it, any less appalling, it does render the tale a bit less mysterious. Lysenko's debate with the Russian Mendelians was, at the outset, a legitimate scientific argument. Later, he held on through fraud, deception, manipulation, and murder-that is the tragedy.

Darwin's theory of natural selection is more complex than Lamarckism because it requires two separate processes, rather than a single force. Both theories are rooted in the concept of adaptation—the idea that organisms respond to changing environments by evolving a form, function, or behavior better suited to these new circumstances. Thus, in both theories, information from the environment must be

transmitted to organisms. In Lamarckism, the transfer is direct. An organism perceives the environmental change, responds in the "right" way, and passes its appropriate reaction directly to its offspring.

Darwinism, on the other hand, is a two-step process, with different forces responsible for variation and direction. Darwinians speak of genetic variation, the first step, as "random." This is an unfortunate term because we do not mean random in the mathematical sense of equally likely in all directions. We simply mean that variation occurs with no preferred orientation in adaptive directions. If temperatures are dropping and a hairier coat would aid survival, genetic variation for greater hairiness does not begin to arise with increased frequency. Selection, the second step, works upon unoriented variation and changes a population by conferring greater reproductive success upon advantageous variants.

This is the essential difference between Lamarckism and Darwinism—for Lamarckism is, fundamentally, a theory of directed variation. If hairy coats are better, animals perceive the need, grow them, and pass the potential to offspring. Thus, variation is directed automatically toward adaptation and no second force like natural selection is needed. Many people do not understand the essential role of directed variation in Lamarckism. They often argue: isn't Lamarckism true because environment does influence heredity—chemical and radioactive mutagens increase the mutation rate and enlarge a population's pool of genetic variation. This mechanism increases the amount of variation but does not propel it in favored directions. Lamarckism holds that genetic variation originates preferentially in adaptive directions.

In the June 2, 1979, issue of Lancet, the leading British medical journal, for example, Dr. Paul E. M. Fine argues for what he calls "Lamarckism" by discussing a variety of biochemical paths for the inheritance of acquired, but non-directed, genetic variation. Viruses, essentially naked bits of DNA, may insert themselves into the genetic material of a bacterium and be passed along to offspring as part of the

bacterial chromosome. An enzyme called "reverse transcriptase" can mediate the reading of information from cellular RNA "back" into nuclear DNA. The old idea of a single, irreversible flow of information from nuclear DNA through intermediary RNA to proteins that build the body does not hold in all cases—even though Watson himself had once sanctified it as the "central dogma" of molecular biology: DNA makes RNA makes protein. Since an inserted virus is an "acquired character" that can be passed along to offspring, Fine argues that Lamarckism holds in some cases. But Fine has misunderstood the Lamarckian requirement that characters be acquired for adaptive reasons-for Lamarckism is a theory of directed variation. 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 happens. If so, it would be an exciting new development, and truly Lamarckian.

But so far, we have found nothing in the workings of Mendelism or in the biochemistry of DNA to encourage a belief that environments or acquired adaptations can direct sex cells to mutate in specific directions. How could colder weather "tell" the chromosomes of a sperm or egg to produce mutations for longer hair? How could Pete Rose transfer hustle to his gametes? It would be nice. It would be simple. It would propel evolution at much faster rates than Darwinian processes allow. But it is not nature's way, so far as we know.

Yet Lamarckism holds on, at least in popular imagination, and we must ask why? Arthur Koestler, in particular, has vigorously defended it in several books, including *The Case of the Midwife Toad*, a full-length attempt to vindicate the Austrian Lamarckian Paul Kammerer, who shot himself in 1926 (although largely for other reasons) after the discovery that his prize specimen had been doctored by an injection of India ink. Koestler hopes to establish at least a "mini-Lamarckianism" to prick the orthodoxy of what he views as a heartless and mechanistic Darwinism. I think that Lamarckism retains its appeal for two major reasons.

First, a few phenomena of evolution do appear, superfi-

cially, to suggest Lamarckian explanations. Usually, the Lamarckian appeal arises from a misconception of Darwinism. It is often and truly stated, for example, that many genetic adaptations must be preceded by a shift in behavior without genetic foundation. In a classic and recent case, several species of tits learned to pry the tops off English milk bottles and drink the cream within. One can well imagine a subsequent evolution of bill shape to make the pilferage easier (although it will probably by nipped in the bud by paper cartons and a cessation of home delivery). Is this not Lamarckian in the sense that an active, nongenetic behavioral innovation sets the stage for reinforcing evolution? Doesn't Darwinism think of the environment as a refining fire and organisms as passive entities before it?

But Darwinism is not a mechanistic theory of environmental determinism. It does not view organisms as billiard balls, buffeted about by a shaping environment. These examples of behavioral innovation are thoroughly Darwinian—yet we praise Lamarck for emphasizing so strongly the active role of organisms as creators of their environment. The tits, in learning to invade milk bottles, established new selective pressures by altering their own environment. Bills of a different shape will now be favored by natural selection. The new environment does not provoke the tits to manufacture genetic variation directed toward the favored shape. This, and only this, would be Lamarckian.

Another phenomenon, passing under a variety of names, including the "Baldwin effect" and "genetic assimilation," seems more Lamarckian in character but fits just as well into a Darwinian perspective. To choose the classic illustration: Ostriches have callosities on their legs where they often kneel on hard ground; but the callosities develop within the egg, before they can be used. Does this not require a Lamarckian scenario: Ancestors with smooth legs began to kneel and acquire callosities as a nongenetic adaptation, just as we, depending on our profession, develop writer's calluses or thickened soles. These callosities were then inherited as genetic adaptations, forming well before their use.

The Darwinian explanation for "genetic assimilation"

can be illustrated with the midwife toad of Paul Kammere Koestler's favorite example—for Kammerer, ironically, performed a Darwinian experiment without recognizing in This terrestrial toad descended from aquatic ancestors that grow roughened ridges on their forefeet—the nuptial pads Males use these pads to hold the female while mating in their slippery environment. Midwife toads, copulating on terra firma, have lost the pads, although a few anomalous individuals do develop them in rudimentary form—indicating that the genetic capacity for producing pads has not been entirely lost.

Kammerer forced some midwife toads to breed in water and raised the next generation from the few eggs that had survived in this inhospitable environment. After repeating the process for several generations, Kammerer produced males with nuptial pads (even though one later received an injection of India ink, perhaps not by Kammerer, to heighten the effect). Kammerer concluded that he had demonstrated a Lamarckian effect: he had returned the midwife toad to its ancestral environment; it had reacquired an ancestral adaptation and passed it on in genetic form to

But Kammerer had really performed a Darwinian experiment: when he forced the toads to breed in water, only a few eggs survived. Kammerer had exerted a strong selection pressure for whatever genetic variation encourages success in water. And he reinforced this pressure over several generations. Kammerer's selection had gathered together the genes that favor aquatic life—a combination that no parent of the first generation possessed. Since nuptial pads are an aquatic adaptation, their expression may be tied to the set of genes that confer success in water-a set enhanced in frequency by Kammerer's Darwinian selection. Likewise, the ostrich may first develop callosities as a nongenetic adaptation. But the habit of kneeling, reinforced by these callosities, also sets up new selective pressures for the preservation of random genetic variation that may also code for these features. The callosities themselves are not mysteriously transferred by inheritance of acquired characters from adult to juvenile.

The second, and I suspect more important reason for Lamarckism's continuing appeal, lies in its offer of some comfort against a universe devoid of intrinsic meaning for our lives. It reinforces two of our deepest prejudices—our belief that effort should be rewarded and our hope for an inherently purposeful and progressive world. Its appeal for Koestler and other humanists lies more with this solace than in any technical argument about heredity. Darwinism offers no such consolation for it holds only that organisms adapt to local environments by struggling to increase their own reproductive success. Darwinism compels us to seek meaning elsewhere—and isn't this what art, music, literature, ethical theory, personal struggle, and Koestlerian humanism are all about? Why make demands of nature and try to restrict her ways when the answers (even if they are personal and not absolute) lie within ourselves?

Thus Lamarckism, so far as we can judge, is false in the domain it has always occupied—as a biological theory of genetic inheritance. Yet, by analogy only, it is the mode of "inheritance" for another and very different kind of "evolution"-human cultural evolution. Homo sapiens arose at least 50,000 years ago, and we have not a shred of evidence for any genetic improvement since then. I suspect that the average Cro-Magnon, properly trained, could have handled computers with the best of us (for what it's worth, they had slightly larger brains than we do). All that we have accomplished, for better or for worse, is a result of cultural evolution. And we have done it at rates unmatched by orders of magnitude in all the previous history of life. Geologists cannot measure a few hundred or a few thousand years in the context of our planet's history. Yet, in this millimicrosecond, we have transformed the surface of our planet through the influence of one unaltered biological invention -self-consciousness. From perhaps one hundred thousand people with axes to more than four billion with bombs, rocket ships, cities, televisions, and computers-and all without substantial genetic change.

Cultural evolution has progressed at rates that Darwinian processes cannot begin to approach. Darwinian evolution continues in *Homo sapiens*, but at rates so slow that it no

longer has much impact on our history. This crux in the earth's history has been reached because Lamarckian processes have finally been unleashed upon it. Human cultural evolution, in strong opposition to our biological history, is Lamarckian in character. What we learn in one generation, we transmit directly by teaching and writing. Acquired characters are inherited in technology and culture. Lamarckian evolution is rapid and accumulative. It explains the cardinal difference between our past, purely biological mode of change, and our current, maddening acceleration toward something new and liberating—or toward the abyss.

8 Caring Groups and Selfish Genes

THE WORLD OF objects can be ordered into a hierarchy of ascending levels, box within box. From atoms to molecules made of atoms, to crystals made of molecules, to minerals, rocks, the earth, the solar system, the galaxy made of stars, and the universe of galaxies. Different forces work at different levels. Rocks fall by gravity, but at the atomic and molecular level, gravity is so weak that standard calculations ignore it.

Life, too, operates at many levels, and each has its role in the evolutionary process. Consider three major levels: genes, organisms, and species. Genes are blueprints for organisms; organisms are the building blocks of species. Evolution requires variation, for natural selection cannot operate without a large set of choices. Mutation is the ultimate source of variation, and genes are the unit of variation. Individual organisms are the units of selection. But individuals do not evolve—they can only grow, reproduce, and die. Evolutionary change occurs in groups of interacting organisms; species are the unit of evolution. In short, as philosopher David Hull writes, genes mutate, individuals are selected, and species evolve. Or so the orthodox, Darwinian view proclaims.

The identification of individuals as the unit of selection is a central theme in Darwin's thought. Darwin contended that the exquisite balance of nature had no "higher" cause. Evolution does not recognize the "good of the ecosystem"