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Darwinian, Spencerian, and Modern Perspectives on Progress in Biological Evolution

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INTRODUCTION

It is currently in vogue in some circles to claim that Darwinian evolution violates a law of decreasing order in the universe, and therefore cannot have occurred (see Patterson 1983). Proponents of this view define evolution as progressive change from simple to complex. Ironically, their view of the universe demands unidirectional change—far more than Darwinism demands progressive improvement. In fact, the argument that evolution means progress from simple to complex is a straw man in a neo-Darwinian context. So it is odd to see an anti-evolutionary argument, however weak in its own right, trying to knock it down. The anti-evolutionists' definition of evolution belongs to the nineteenth century. But not, significantly, to Charles Darwin.

This definition of evolution is largely Spencerian. Darwin's contemporary Herbert Spencer did indeed view evolution as progress from simple to complex. He also claimed to have anticipated Darwin in the discovery of natural selection. He too had been reading Malthus; he too had derived from Malthus a principle of selection based on competition. But in reality, Spencer's selection differed from that of Darwin, as did his vision of evolutionary progress. In fact, ornithologist and evolutionary historian Ernst Mayr, in his treatise on the history of evolutionary biology, refused to admit any role for Spencer in the development of evolutionary biology (Mayr 1982). To Mayr, Spencer was merely a contemporary of Darwin who had misconstrued biology in general and misapplied Darwinism in particular to social evolutionary change. He was also a man who had received undue praise for his contributions to evolutionary biology during his own lifetime (for example, Buckley 1892). Yet even before his death in 1903 Spencer's reputation had considerably declined. Evolutionary biology was no longer Spencerian. In large part, Mayr insists, it never was.

This negative appraisal of Spencer's impact on evolutionary biology is not
Herbert Spencer was an evolutionary progressionist. Underlying his vision of evolutionary progress was a defense of individualism that was to emerge, under the label Social Darwinism, most clearly in the laissez-faire economics of the 1880s. Spencer opposed all forms of socialism as unwarranted political interference with individual freedom. His grandiose theory of social evolution posited that the "right," or most "fit," people would survive and that order and perfection would be achieved through natural evolution.

Spencer's idea of fitness was imbued with nineteenth century notions of desirability and value, and it is impossible to read Spencer today without noticing the extent to which social prejudices affected his interpretation of progress. Eggs--the sex cells produced by women--could not play any role in the coordination of development; development must be directed instead by sperm, which must therefore figure more prominently in evolutionary progress! Australian aborigines must have body proportions that are less advanced--less "heterogeneous"--than those of Europeans! One biographer commented that we now approach Spencer as we might approach an "outmoded encyclopedia, ...not expecting to find what is right, but rather to review errors that were plausible a century ago" (Kennedy 1978:7). It was, however, precisely those errors that made him so attractive to his elite European contemporaries. He told them what they wanted to hear; he built a dream--a Victorian gentleman's vision of the best of all possible worlds. And then he assured his readers that this dream had to come true. In fact, his Utopia was very like that constructed by anti-evolutionists, except that the latter insist that God must intervene, and Spencer insisted that progress was guaranteed by natural law.

From early in his career, Spencer defended the inevitability of progress. Common features of diverse manifestations of progress must describe a law that could be used to predict the future. Since perfection, as Spencer imagined it, was not manifest in his own world, all of the steps leading to perfection could not have occurred yet. They would in time, however, for "progress is not an accident, not a thing within human control, but a beneficent necessity" (1910:60).

In an essay called "Progress: Its Law and Cause," Spencer's general doctrine of evolution made its first appearance. The concept of selection was not discussed in it, although this essay was published five years after Spencer had first introduced selection as a proximate cause of progress. Indeed, biological evolution was of little concern in this essay. It merely provided one, not terribly strong, example of progressive evolution. Evolution comprised all change from simple to complex--all progress, in other words. Progress could be manifested in any of numerous forms: in the development of an individual; in the geological development of the earth; in the history of society,
government, manufacture, commerce, language, literature, science, and art; and in the fossil record of biological life. Spencer sought a law that would guarantee the ultimate attainment of human happiness, and he thought he found it in von Baer's "law" of ontogenetic development. Organic progress comprised change from "homogeneous to heterogeneous," from simple to complex, from the uniform germ cell to the differentiated adult organism. "From the earliest traceable cosmical changes down to the latest results of civilization," Spencer wrote, "we shall find that the transformation of the homogeneous into the heterogeneous, is that in which progress essentially consists" (Spencer 1910:10).

Once Spencer had formulated his law of all development, he needed to find a principle that would produce heterogeneity from homogeneity. Since progress or evolution comprised more than biological transformation, this principle could not be strictly biological. Furthermore, since it was widely held in the nineteenth century that general laws of development could be found that applied across all disciplines, there was no need to construct a biological explanation for biological change. This is why Spencer invoked physical forces to explain evolutionary change, and this is one of the reasons why natural selection was always, to Spencer, a secondary cause of evolutionary change. Spencer argued that increasing complexity was the necessary consequence of active forces, their persistence and cumulative effects. Thus, he believed, trees develop from seeds, animals develop from fertilized ova, and European limb proportions develop from those of Australian aborigines, all because of "disturbing forces." Biological modifications are brought about by "mechanical conditions" or "muscular forces." Such modifications are transmitted to offspring through the inheritance of acquired characteristics--a notion compatible with the idea that the cumulative effects of force must persist.

Today this seems a naive and superficial argument, especially in light of the specific examples this law was supposed to explain. (Do "forces acting" really predict that Australian aborigines will have "less heterogeneous" body proportions--whatever that means--than Europeans?) But to Spencer, both the generalization that all progress consists of the transformation of the simple into the complex and the explanation that this is due to the persistence of force were central truths. From physical principles--the "indestructibility of matter," the "continuity of motion," and the "dissipation of motion"--Spencer attempted to derive all laws of change, and, in so doing, to prove the inevitability of human perfection.

Thus a set of physical principles became Spencer's First Principles (1862); they predicted universal parallel transformations. When, during Spencer's lifetime, it became evident that germ cells are not homogeneous in structure and chemical composition, he was nevertheless reluctant to relinquish his law of universal development. This concept was the key to his First Principles--and it was from laws of the highest order of generality that he derived all other generalities. The doctrine of universal transformation was part and parcel with Spencer's definition of evolution. Matter tends to become integrated, Spencer wrote; motion to become dissipated. Put matter and motion together and you get greater coherence of individual parts, and more parts. Using such arguments Spencer could make the division of labor in society comparable to the multiplication of cells in an individual organism, or to the diversification of all biological life (each involved more "individual" parts). He wrote:

Evolution is an integration of matter and concomitant dissipation of motion; during which the matter passes from a relatively indefinite, incoherent homogeneity to a relative definite, coherent heterogeneity, and during which the retained motion undergoes a parallel transformation [cited in Elliot 1970:244].

This definition of evolution is decidedly nonbiological. In Spencer's world, biological evolution was but one manifestation of a broader process of change. And selection was but one process that would aid the development of life on earth. Darwin constructed a theory of change by natural selection, according to which general progress was one possible consequence; Spencer constructed a theory of progress according to which selection, and indeed, biological evolution, were possible consequences.

**SPENCER'S SELECTION**

Use inheritance, Spencer's preferred mechanism of biological evolutionary change, was rejected by most biologists after the publication of Weismann's germ theory in 1883. Darwin had accepted use inheritance, although he defended natural selection as the primary mechanism of evolutionary change. Spencer, on the other hand, was never an ardent
defender of natural selection; and after the publication of Weismann's germ theory threatened to destroy the foundation of his own preferred mechanism of evolutionary change, he intensified his critique of selection and elevated use inheritance to a primacy that even he had not advocated before (Kennedy 1978). Only late in his life did Spencer claim priority for having discovered natural selection in human populations, and only then did he lament having overlooked the "obvious corollary" that selection must be a "universally-operative factor in the development of [all] species" (1904:451):

"Theory of Population" was one of several early Spencerian statements about the nature of progress. It concerned the implications for human progress of the so-called law of animal fertility. But rather than failing to generalize or to consider organisms in general, this essay begins with the simplest organisms and attempts to generalize to humans. Darwin's theory of natural selection is not there, not because of an oversight, not because the focus was too narrow, not because Spencer believed the inheritance of acquired characteristics sufficient to explain organic evolution; but because, conceptually, Spencer's selection was different from that of Darwin. It would be impossible to derive Darwinian selection from it.

That is not to say that there are no similarities between Darwin's concept of natural selection and the selection Spencer described in "Theory of Population." Both Darwin and Spencer developed a principle of selection based on Malthus. Both were members of a community of scholars writing about the so-called population problem--Malthus's supreme dilemma and "justification" for social injustice (Chase 1980). The phrases struggle for life, self-preservation, competition, and overproduction were not concerns of Darwin alone, but of an entire academic world to which both Darwin and Spencer belonged. Like Darwin, Spencer used competition and overproduction to make an argument for rather than against evolutionary change. Both Spencer and Darwin reversed the prevailing view that the struggle for life preserved the integrity of species by eliminating the unfit (contrast Darwin and Spencer with William Kirby, John Crawford, and, indeed, Malthus himself; see Jones 1980). But the similarities between Spencer's and Darwin's original formulations of selection end here.

Spencer's law of animal fertility was, like many other Spencerian laws, a loose empirical generalization based on a limited and carefully selected sample of observations. Specifically, it was based on the observation that simple organisms,
such as bacteria, reproduce very rapidly and in
great quantities but produce short-lived offspring;
whereas more complex organisms, such as mam-
mals, tend to produce few offspring, each of which
has greatly enhanced powers of self-preservation
and therefore greatly enhanced chances of surviving
for a long period of time. From this Spencer
derived a law that he took as characterizing the
Great Chain of Being—that there is an inherent
necessary opposition between individuation (that is,
self-preservation, complexity, coordination, capacity
for self-regulation) and reproduction (that is,
fertility). In order to advance along the ladder of
life, Spencer thought, there must be some sacrifice
in the realm of reproduction. Thus, Spencer
believed that it was not possible to advance in the
realm of individuation without simultaneously
experiencing a decline in fertility. (A similar
though not identical argument was offered in his
Principles of Biology, Vol. II, 1867.)

Spencer liberally applied his law to a variety of
biological and social phenomena. For example,
sperm cells provided Spencer with one arena for a
battle between individuation and reproduction.
Since, Spencer thought, eggs could contain only
material "to be coordinated," sperm must be
responsible for coordinating the growth of the
nervous system and thus must possess remarkable
powers of individuation. Such powers could be
enhanced only at the expense of reproduction—that
is, decreased production of sperm cells. Spencer
argued that in sustaining this natural antagonism
between reproduction and individuation, sperm
cells must strike a delicate balance, sacrificing
fertility for greater efficiency in individuation.

Another application of the law of animal
fertility was to the problem of perfection in human
social and economic life. It was in this section of
his essay that Spencer erected selection as a
proximate cause of progress.

Spencer argued here that humans had not yet
achieved ultimate perfection since human
populations were still plagued by excess fertility.
As long as excess fertility existed, there was room
for its reduction; and as long as there was room for
reduced fertility, increased individuation could
occur. It was in this sense that Spencer posited
excess fertility as a problem for human populations,
and it was in this sense that he viewed population
pressure as a "proximate cause of progress" (or of
individuation). Stated in this way, Spencer's early
formulation of selection looks very non-Darwinian,
and also very nineteenth century. And as might be
anticipated, Spencer envisioned that this increased
individuation would be manifested in human
anatomy as well as in social behavior.

The argument went like this: Population
pressure poses a problem whose solution necessi-
tates technological or industrial advance—that is,
improvements in the skills of self-preservation.
One improves one's own and one's family's chance
of survival (self-preservation) by increasing
industrial or agricultural production (most definite-
ly not by increasing fertility). Premature death
comes to those who fail to contend in this way with
the problem of population pressure. Thus, the
proximate cause of progress is excess fertility.
Given excess fertility, there is necessarily competi-
tion, and given competition, there is necessarily
improvement in skill by selection. Those males "in
whom the power of self-preservation is the greatest"
will be "the select of their generation." In other
words, they will exhibit a prescribed and predictable
set of improvements—prescribed and predictable
not because selection is operating under specific
environmental conditions, but because of a law that
requires all improvement to be unidirectional.

It was only after Spencer had described all of
the presumed manifestations and ramifications of
individuation that he felt ready to predict future
change. The "select of their generation" would
have bigger brains, would have heightened senses of
morality, and would be less fertile than those in
whom the "power of self-preservation" was the
least. "So long as there is pressure on the means of
subsistence," Spencer wrote (1852:267), "further
mental development must go on, and further
diminution of fertility must result."

This rather startling conclusion is but a short
step from the next, and perhaps least Darwinian, of
Spencer's deductions—that selection generated by
population pressure or the struggle for life would
be the vehicle of its own eradication. Selection, as
originally formulated by Herbert Spencer, was a
self-destructive process!

Spencer reasoned that intellectual, moral, and
physical improvement could not accrue forever, just
as fertility cannot decrease ad infinitum, since such
decrease would threaten the extinction of the
population. But according to Spencer's law, with-
out a concomitant decrease in fertility there could
be no progress in the realm of individuation. "For
a cessation in the decrease of fertility implies a
cessation in the development of the nervous
system." Spencer did not see this as a problem,
however, since

this implies that the nervous system has
become fully equal to all that is demanded
of it—has not to do more than is natural to
it....In the end the obtainment of subsistence will require just that kind and that amount of action needful to perfect health and happiness [Spencer 1852:267].

Spencer believed that, once the human population produced only enough offspring to sustain itself, Utopia would have emerged. There would be no further suffering, no further evil. Virtually no youth would succumb to disease or to accident, and the powers of self-preservation of those born into this world would be as perfect as possible. The population would have increased to the maximum possible to comfortably people the globe. Inferior, lazy races would have disappeared, and no further evolution would be possible. Here was the making of the perfect human type—one that satisfied the prejudices of the Victorian world.

Interestingly, Spencer's conclusion that decreased fertility would solve Malthus's population problem was not unique. Indeed, as Nisbet (1980) has shown, Malthus himself had come to this conclusion in late versions of his famous essay. Perhaps Spencer's most striking distinction was that he couched his argument in terms of a biological law—of necessity rather than opportunity. This was in part why Spencer was so esteemed in the nineteenth century, when every scholar's goal was to discover those few laws from which, presumably, everything could be logically derived. But it did not make Spencer's essay strikingly Darwinian; Darwin did not hang selection on a law of necessary antagonism between individuation and reproduction.

The wide acceptance of Spencer's argument of scholarly priority is most curious, particular in light of the proclivity of Darwinian biologists to equate selection with differential reproduction and to consider increases in fertility and fecundity advantageous. Spencer's early concept of selection was in some ways antithetical to Darwinian selection as currently understood.

Of course Spencer's selection did involve differential survival—the differential survival of acquired traits. To Spencer, there was no question that greater industriousness, larger brains, and less inclination to reproduce, would be inherited. The conscious choice to work hard in the face of population pressure would effect behavioral and physical changes that would be passed on through use inheritance to offspring. Spencer never considered it possible that people with many offspring could be the "select of their generation." The "select" must be disinclined toward the physical act of reproduction itself. To the "select,"

pleasurable activities would be those of the mind.

In summary, when Spencer wrote that population pressure is the cause of progress, he meant, first, that it is the problem that humans must strive to overcome; and second, that it is the mechanical cause of a competitive struggle that must result in differential survival. Difficulty in getting a living stimulates improvements in industrial and agricultural production. Individuals strive toward self-preservation. Those who seek to solve the population problem by improving their own lot through hard work will succeed, and their success will be manifested in biological changes that are inherited. Their offspring will inherit larger brains, greater skill, intelligence, self-regulation, and self-satisfaction, as well as reduced fertility!

Spencer's selection was far more deterministic than that which Darwin was to propose seven years later. How could Spencer's selection explain variation in human pigmentation or the shape of the beak of finches? Spencer did not frame selection as a vehicle of variable, adaptive change. He had not merely failed to extend his concept beyond humans; he had failed to apply it to human adaptive diversity.

Even late in his lifetime, after he had incorporated a more Darwinian concept of selection into his work, Spencer clung to a vision of unilinear progress. Selection was always a means to achieve supreme order and stability in human society. It was always a means toward perfecting the human type.

To his credit, in his Autobiography, Spencer (1904) acknowledged his failure to consider adaptive variation; he realized that there lay the key to Darwin's resolution of the population problem and particular formulation of selection. The fact remains, however, that in 1852, Spencer had not devised a concept that could account for adaptive diversity—human or otherwise. This was, of course, Darwin's central concern in his Origin of Species.

**DARWIN'S GENIUS**

It may seem odd to say that one can recognize genius in ambivalence. Yet skepticism is the stuff of scientific advance, and it is all the more impressive when it challenges a belief that has become entrenched in the scholarly literature. Such was the belief in progress. When Darwin wrote The Origin of Species, the belief in progress dominated far more than the discipline of biology; it dominated all fields of natural, social, and physical science, as well as the humanities. The second half of the nineteenth century was the heyday of the idea of
progress (Bury 1932; Nisbet 1980). Charles Darwin was a product of that age. He was certainly an evolutionary progressionist, but he was also one of the most severe critics of the "law" of progressive development. This is why Gould (1977:13) has maintained that "an explicit denial of innate progression is the most characteristic feature separating Darwin's theory of natural selection from other nineteenth century evolutionary theories." Darwin only weakly defended the best accepted standards of overall advance in organization. He found problematic both von Baer's criterion of increased complexity and Milne Edwards's criterion of increased specialization in function of organs.

The difficulty Darwin experienced in accepting any single standard of progress in the biological world stemmed from his acute sense that the pattern of diversification does not describe a simple pattern of increase in any one thing, and also from his awareness that the theory he had developed did not require it. Natural selection was Darwin's agent of progress; yet he had defined it in such a way that progress could not be a necessary consequence. Natural selection was a mechanism whereby fitness--an organism's adaptation to a particular environment--is enhanced. In other words, natural selection was, to Darwin, an agent of local adaptation. Furthermore, although Darwin left the causes of variation undefined, he was explicit in his belief that natural selection must work with variation produced by some process independent of selection itself. If beneficial variants are not somehow a priori produced; or if there is no modification in the physical or biotic environment providing an incentive (or pressure) for improvement; or, finally, if certain existing complex adaptations are no longer needed in a changed or newly occupied environment; then it follows that progress may not occur. It is even possible that retrogression in the scale of organization will occur. In a nutshell, if different environments require different adaptations, Darwin's theory provided no clear standard by which an organism from one environment could be judged superior to an organism from another. Indeed, it provided no clear standard by which they could be compared. Darwin wrote:

We can see, bearing in mind that all organic beings are striving to increase at a high ratio and to seize on every unoccupied or less well occupied place in the economy of nature, that it is quite possible for natural selection gradually to fit a being to a situation in which several organs would be superfluous or useless: in such cases there would be retrogression in the scale of organization [Darwin 1963:105].

Also:

On our theory the continued existence of lowly forms offers no difficulty; for natural selection, or the survival of the fittest, does not necessarily include progressive development--it only takes advantage of such variations as arise and are beneficial to each creature under its complex relations of life [1963:105].

By asking how much the level of organization had actually tended to advance, Darwin converted the general truth of progress into a hypothesis demanding more data for verification. He acknowledged that his hypothesis that organization on the whole should advance under natural selection had not yet been adequately tested, and he admitted practical difficulties in testing it. There were, for example, difficulties in ranking "high" and "low" when comparing biota from different areas or from different times, or in comparing organisms exhibiting very different organizational plans. "Who will decide," wrote Darwin (1963, p. 337), "whether a cuttle fish be higher than a bee?" In their own worlds, barnacles, parasites, and earthworms are as perfect as are horses, falcons, and people. What's more, Darwin marshalled evidence to show that general progress had not, indeed, universally occurred, and that the pattern of diversification produced by natural selection was hard to interpret in terms of a simple polarity between low and high or simple and complex. Darwin went so far as to say that if one insists that his theory demands that progress must occur, one is then forced to consider his theory falsified! Progress (in the sense of overall advance in organization) is a prediction, but not a necessary consequence, of natural selection. Perfection in a local context and overall advance in organization are not the same thing. Under specific environmental conditions, overall advance in organization could not be expected to occur.

Darwin's theory was an optimization theory based on context-specific competition. He talked about natural selection producing increasingly complex organisms, or increasingly reproductively successful organisms, or organisms with increasingly bigger brains. But he left only one criterion for judging overall fitness--competitive success within specific environmental contexts. The metaphors he used, including those he borrowed from Spencer...
was willing to defend evolution without vectorial view of the universe. The reluctance of shall see.

...unwillingness to recognize more than net progress of different sorts in different evolutionary lineages, and their general refusal to equate evolution with progress of any sort, are direct consequences of the Darwinian paradigm. Modern neo-Darwinists do not depart radically from Darwin's ambivalence toward the concept of overall evolutionary progress.

MODERN INTERPRETATIONS OF PROGRESS: NEO-DARWINISM

Progress does not have a single interpretation in the neo-Darwinian paradigm. Most neo-Darwinists agree that there is no standard by which uniform progress can be said to have taken place (Simpson 1974; Ayala 1974, 1977). Evolution is too erratic. But neo-Darwinists also believe that net progress has occurred, and that progress can only be understood in a Darwinian context. Progress is not possible without selection, although selection does not necessarily result in progress. Selection, while not directed, gives direction to evolution. That direction results either in adjustment to local conditions (perfection in the sense of better local adaptation), or in improved capacity to compete under a variety of circumstances (perfection in a more general sense). Directional evolution is said to occur without progress if, despite long sustained directional change, terminal members of a lineage are not "better off" in some general sense than early members of the same lineage. Spatial clines may exhibit adaptive fine-tuning whereby individuals at opposite ends of a geographic range are adapted to entirely different environments, but individuals at neither end are more progressive than the others.

Similarly, temporal gradients may exhibit the same kind of directional change without general improvement. General progress is said to occur when later members of a lineage acquire true improvements. There have been repeated attempts to find simple quantities that may improve in such a manner as a result of natural selection. Such a quantity may be defined as a function of optimization processes or as a consequence of long-term competition. Fitness will be optimized during natural selection; therefore, one has to discover the properties of greater fitness. What has emerged is a multifocal definition of general progress. There are many standards of progress, and all of them are believed to accrue as a function of natural selection. Competition will result in broader ranges of adaptive response to adversity; it will result in increased homeostasis, improved potential for reproductive success, increased complexity, increased efficiency in the utilization of limited resources, and so on. Even adaptive diversification has been attributed to natural selection (although clearly other factors are also involved, at least in the multiplication of lineages).

What has also emerged in the neo-Darwinian
literature is the sense that none of these standards is entirely satisfactory as a criterion for general progress, because increases in a given direction will not always give species a competitive advantage. Take, for example, increases in the range of adaptive response. Generalists display adaptive flexibility; yet when resource diversity is low, a generalist adaptive strategy is not successful—specialists are better able to utilize the ubiquitous, if monotonous, available foods. Similarly, complexity is not always beneficial. Simple parasites do quite well by taking advantage of the vital life services provided by their hosts. Greater metabolic efficiency may not be a good standard under all conditions; one can easily envision circumstances under which new metabolically expensive adaptations will be selected in order to attain some other advantage. It seems that even general criteria of progress cannot be applied universally. Modern Darwinism recognizes, just as Darwin did, that the theory of natural selection implicitly prohibits a single best criterion for progressive change from being formulated.

Standards of progress appear ad hoc or axiological. George Gaylord Simpson has stated this eloquently, concluding a review article entitled "The Concept of Progress in Organic Evolution" with the following observations:

Some organisms are better than their ancestors or than some of their relatives at doing certain things in certain ways. Some oysters are better at being oysters than their ancestors. Some trees are better at living on mountain tops than others. We are doubtless better at being men than Australopithecus was, although I go along with Haldane far enough to believe that monkeys are better at being monkeys than we would be even if we tried. It is also true that sometimes whole groups have been carried by selection to a point where their great expansion into various adaptive zones became possible, a progressive feature of evolution....That is the explanation, in unduly broad terms, of the spread of dominant groups from time to time.

With such examples it is perfectly reasonable to say that improvement has factually occurred and that there is therefore evolutionary progress. The progress is, however, ad hoc in every case. Our ancestors' progress was not the oysters', the trees', or the monkeys', nor was theirs ours. Since we are humans, after all, the most interesting and important progress is progress toward us, but let us not mistake this for a general phenomenon.

Probably the most important result of this somewhat dispersive inquiry is negative: there is no innate tendency toward evolutionary progress and no one, overall sort of such progress. We cannot sit back and assume that natural selection will lead to progress for us, or for anything else. We cannot even assume that prolongation of past progress would continue to be progress [Simpson 1974:50-51].

Francisco Ayala (1977:516) draws a similar conclusion: "Organisms are more or less progressive depending on what criterion of progress is used. By certain criteria, flowering plants are more progressive than many animals." Homo is only the "most perfect" of organisms if one chooses one's standard of progress accordingly. But such a standard as "the ability to perceive the environment, and to integrate, coordinate and react flexibly to what is perceived...is not necessarily better or worse than other criteria of progress" (Ayala 1977:516).

So progress is ambiguous in a neo-Darwinian context, and neo-Darwinism simultaneously claims and disavows it. Neo-Darwinists certainly do not equate progress with evolution, as some anti-evolutionists have claimed. Even if we could find some one quantity that increases with time as a result of natural selection, we would have to assess the relative importance of that increase as opposed to other kinds of evolutionary change before evolution could be equated in any sense with progressive change.

Recently the adequacy of neo-Darwinism to explain different forms of progress has been challenged on other grounds. Progress has not only diverse meanings, but also diverse causal mechanisms.

MODERN INTERPRETATIONS OF PROGRESS: NON-DARWINIAN FRAMEWORKS

Perhaps the least radical of the challenges comes from proponents of the theory of punctuated equilibria (Eldredge and Gould 1972; Stanley 1975, 1979; Gould and Eldredge 1977; Gould 1980; Eldredge 1985a,b). Their argument is less a challenge to the importance of Darwinian selection as a driver of evolutionary trends than it is a challenge to the primacy of the narrower neo-Darwinian reformulation of selection—that is, "natural selection" as mathematized and...
conceptualized by the founders of the "Modern Synthesis." The "Modern Synthesis" refers to the melding of Darwinism and particulate ("beanbag") genetics that occurred in the 1930s largely through the efforts of geneticists such as Haldane, Fisher, Wright, and Dobzhansky (see Fisher 1930; Dobzhansky 1937; Mayr 1942).

The growth and acceptance of beanbag genetics gave new meaning to natural selection and to evolution in general; evolution was now temporal change in gene frequency, brought about through the differential survival and reproduction of individuals belonging to single species. Selection operating at higher levels (for example, among breeding populations or whole species) was deemed unimportant, despite the fact that Darwin had considered competition at multiple levels very much a part of the normal operation of natural selection. The neo-Darwinian focus on individuals developed not directly from Darwin's work but from the synthesis of Darwinian naturalism and population genetics. Neo-Darwinism was a theory of genes which tied the ultimate survival of genes to the differential survival of their individual hosts. By the 1970s, sociobiologists—perhaps the staunchest, least compromising of modern defenders of neo-Darwinism—had begun criticizing the Synthesis for not taking gene theory far enough. To sociobiologists, selection acts at the level of "selfish," competitive genes and can in fact thwart the selfish interests of the individuals carrying them (viz., the evolution of all forms of altruism, which sociobiologists take to be genetically controlled; Wilson 1975; Dawkins 1976, 1986).

Of course, one need not resort to beanbag genetics to justify, within a Darwinian paradigm, an emphasis on differential survival of individuals (rather than of populations or species). If competition is the fundamental component of natural selection operating at any level, then in order to discover the level at which natural selection most frequently operates we might ask where we would expect to find the most severe competition. The intensity of the "struggle for existence" should depend on the similarity of the competing individuals as well as the extent of their overlapping requirements. Because members of the same genus tend to resemble each other more than do members of different genera, congeneric competition should be greater than competition between species of different genera. Competition between individual members of the same species should be the most severe.

But proponents of the theory of punctuated equilibria argue, contra neo-Darwinism and sociobiology, that long-term macroevolutionary trends are less a product of the differential success of individuals belonging to single species than of differential production and success of whole species. They claim that competition between individuals within species, at least during the vast majority of the existence of most species, will lead to fine adaptive adjustments but rarely to long-term directional trends of the sort that may be identified as progressive (Gould 1980; Stanley 1981; Eldredge 1985a, 1985b, 1989).

Punctuationalists base this claim on the postulate that rapid phenotypic evolution most often occurs under conditions that are also, incidentally, conducive to the generation of new lineages (for recent discussions, pro and con, see Eldredge 1985b, 1989; Vrba 1985; Hoffman 1989; Levinton 1989; Otte and Endler 1989; Godfrey and Marks 1991; Kimbel and Martin 1993). Speciation (the multiplication of lineages) generally occurs because small populations have become geographically isolated and genetically separated (e.g., due to karyotypic changes that initiate reproductive isolation) from their parent populations (White 1978; Godfrey and Marks 1991). Furthermore, small populations facilitate the fixation and spread of evolutionary novelties generated not solely by selection but also by stochastic processes.

Thus, punctuationalists argue, it is the process of speciation per se, and not the intensity of competition between individuals, that produces rapid morphological evolution. Indeed, it has been suggested that periods of relaxed (rather than intense) competition may occur in association with speciation, and that such relaxed selection may allow the survival of novelties that would not otherwise survive. Finally, punctuationalists argue that if the factors affecting evolutionary change during speciation differ from the factors affecting evolutionary change in whole lineages, we cannot predict evolutionary trends as products of the constant adjustment of individuals to their changing environments. Speciation trends (that is, trends associated with the differential production or survival of species) may have little in common with trends associated with the differential survival of individuals belonging to single species (Stanley 1979). The relative competitive success of a species may ultimately depend on events that occur in a short period of time during its origination. This of course throws wide open the question of whether selection as used by neo-Darwinists drives "progressive" evolution! It seems that, to sort this out, we must build a hierarchical model of
evolution, in which selection is free to act at multiple levels and independent directional trends can be produced at those different levels, with concomitant upward and downward effects (Gould 1980; Vrba 1984; Vrba and Eldredge 1984; Eldredge 1985a,b).

A more basic challenge to the tenets of neo-Darwinism has come from evolutionists who reject the notion that directional trends are the product of selection operating at any level (see, for example, Saunders and Ho 1976, 1981; Ho and Saunders 1979, 1984; Katz, 1982, 1987). They argue that classic examples of evolutionary progress driven by selection (including increases in complexity) can be understood without reference to either optimization theory or competition. Instead, they offer a theory that examines the properties of biological systems and the internal developmental constraints on the direction of evolutionary change. An optimization model that predicts merely that "advantageous" changes will occur is, at the very least, incomplete.

It is the poorly understood link between the genome and the phenotype that so fascinates these investigators. While neo-Darwinism has been strongly influenced by population genetics, it has remained relatively uninfluenced by experimental embryology or physiological genetics (Raff and Kaufman 1983; Arthur 1987). Yet phenotypes arise only indirectly from genes; they arise through the interactive process of development. What is often missing from genetic models of phenotypic evolution (and also from attempts to link particular genetic or chromosomal structural changes to radical morphological change) is the bridging argument from physiological genetics (Godfrey and Marks 1991; Marks 1992). Non-Darwinian evolutionary biologists such as Mae-Wan Ho and Peter Saunders have long maintained that biologists cannot understand the pattern or directionality of evolutionary change unless more attention is paid to how epigenetic systems work (that is, the interactions between the genome, the cellular environment in which the genome operates, and the external environment in which development of the organism as a whole takes place). It is like trying to predict patterns of change in computer programs without understanding the language (the subroutines, built-in functions, and mathematical identities) in which the programs are written (Saunders and Ho 1981). If we want to understand potential modifications of a computer program, Ho and Saunders argue, it is far more useful to learn the language than to build expectations based on a naive optimization model. (See Katz 1982, 1987, for an application to the problem of the evolution of the human brain. For a radical exposition of this evolutionary perspective, see Lima-de-Faria 1988.)

Non-Darwinian biologists insist that it is not sufficient to view evolution as change in gene frequency, or even as change in the genetic blueprint for development. Such a paradigm, they argue, fails to consider how directions of evolutionary change are influenced by the structure of the genome, genetic redundancy, and epigenetic interactions. Using a Darwinian predictive framework alone, one can imagine that changes in all directions are generated by "random" mutations and that the actual direction of change is limited only by competitive advantage. Individual competition is ubiquitous and sufficient to make natural selection a constant viable force, generation after generation. However, some field studies have suggested that competition may not be as important as Darwin and his contemporaries believed (for example, Wiens 1983). Perhaps competition only matters during resource crunches and selection operates intermittently in populations in general. Furthermore, it is abundantly clear that the variations on which natural selection works are not random. To the extent that they themselves are patterned and predictable, they will impart some directionality to evolutionary change (Ho and Saunders 1979; Saunders and Ho 1981; Bonner 1982). Finally, there is the (alas! seemingly neo-Lamarckian) suggestion that cytoplasmic inheritance may be involved, at least in the initial stages of fixing new epigenetic pathways (Ho and Saunders 1979; Saunders 1985). If so (and the evidence for this is far from conclusive; Maynard Smith 1982), we have yet another agent of directional and progressive change (see Arthur 1984, 1987 for a discussion of the normal operation of cytoplasmic inheritance).

So progress has changed considerably from its nineteenth century Spencerian formulation. To Spencer, progress was a law of all evolutionary change--a law of increasing complexity that was also strongly associated with "fitness for the conditions of life" and with the attainment of the ideal type. Natural selection was a consequence of progress, although not its sole cause. To Darwin, progress was a consequence of natural selection, although not a necessary consequence. Neo-Darwinists treat progress essentially as Darwin did, although it has become more openly multifocal and, to some leading neo-Darwinists, ad hoc. Some non-Darwinian evolutionists now argue that the notion of increasing complexity must be divorced from the...
notion of selection or fitness. Increases in complexity, long believed to be a major indicator of progressive or advantageous change, may follow automatically from the way in which the epigenetic system operates. Complexity is probably not best conceived as a measure of fitness, but as a measure of the information content of developmental building instructions. It will not necessarily increase as a function of optimization. Phenotypic changes will not occur randomly, but will depend on the existence of alternative developmental pathways that can accommodate them. At issue is the probability of the occurrence of changes in different directions.

What has been called progress, then, is quite probably the product of a host of factors, only one of which is the natural selection of individuals belonging to single lineages. And evolution is not merely progressive change!

NOTES

1. Jones (1980) points out that Spencer actually agreed with Kirby and Crawfurd that the struggle for existence preserved the type of species. But Spencer argued that the struggle would lead to constantly improving that type, and in this sense to "evolutionary" change. John Crawford's view of the struggle for existence was more typical. Witness this statement made in an address to the Ethnological Society of London ten years after the publication of Darwin's Origin: "As to 'the struggle for life,' there is no doubt that, through all living beings, it is the weak that perish and the vigorous that survive. Nature, in some cases, takes some pains for preserving the integrity of the species but never for its improvement by mutation" (Crawford 1869).

2. The Synthesis views the genome essentially as a bag of independently sorting "strings of beads." Genes, the fundamental units of replication (DNA to DNA), transcription (from DNA to RNA), and translation (from RNA to protein), comprise the beads on chromosomal filamentous strings. It is now known that the genome is far more complex than this implies. For example: The units of DNA replication ("replicons") are not the same as units of RNA transcription ("genes"). Strings of DNA can be spliced and transcribed in alternative fashions; therefore the boundaries of genes are not stable. Most of any DNA sequence that is transcribed into RNA is not subsequently translated. There is an enormous amount of redundancy (repetitive elements) within the genome. There are also long strings of "silent" (non-coding) DNA both within and between genes. These can evolve quickly because their molecular structure can change without producing deleterious consequences for the phenotype. Only approximately 1% of the genome is coding. The genome has promoters and binding sites that are essential to the development and functioning of the organism but are never transcribed; it is not clear whether these should be called genes. Two essential questions, the relationship between "genes" and "characters," and the effects of the structure of the genome on the production of phenotypes, remain unsolved. Marks (1992) reviews the demise of "beanbag" genetics, and how advances in molecular genetics may affect evolutionary theory.

REFERENCES

(1974) CA* Comment on "The Evolutionary Theories of Charles Darwin and Herbert
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