have combined simulation of behavior and morphology to automatically evolve and construct actual robots. Further work by Murata and Yamaguchi (2005) employs genetic algorithms to self-configure robots that can assemble and repair themselves in simple situations.

The parallels between biological evolution, searching through a space of genotypes, and computer evolution, searching through a space of computer programs or other data structures, have crystallized to create the scientific enterprise of evolutionary computing. This field has proven useful in a variety of commercial optimization problems, showing promise for many complex scientific and engineering problems.

BIBLIOGRAPHY

Fogel, D. B. 1998. *Evolutionary Computation: The Fossil Record.* New York: IEEE Press.

Holland, J. H. 1992. *Adaptation in Natural and Artificial Systems: An Introductory Analysis with Applications to Biology, Control and Artificial Intelligence.* Cambridge, MA: MIT Press.

Koza, J. R. 1992. *Genetic Programming: On the Programming of Computers by Means of Natural Selection.* Cambridge, MA: MIT Press.

Lipson, R., and J. B. Pollack. 2000. Automatic design and manufacture of robotic life forms. *Nature* 406: 974–978.

Mitchell, M., and C. E. Taylor 1999. Evolutionary computation: An overview. *Annual Review of Ecology and Systematics* 30: 593–616.

Murata, T., and M. Yamaguchi. 2005. Neighboring crossover to improve GA-based Q-learning for multi-legged robot control. Paper presented at the Proceedings of the 2005 Conference on Genetic Evolutionary Computation, Washington, DC, June 25–29.

Rechenberg, I. 1973. *Evolutionsstrategie: Optimierung Technischer Systeme und Prinzipien der Biologischen Evolution.* Stuttgart: Frommann-Holzboog.

Turing, A. 1950. Computing machinery and intelligence. *Mind* 59: 433–460.

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Evolutionary Progress

Modern organisms seem clearly more advanced than ancient ones. Compare an elephant with a modern bacterium. (The comparison is apt in that certain modern bacteria are probably very similar to the first fossil organisms known, from rocks 3.5 billion years old.) The notion of an ordering among organisms dates at least to Aristotle, who arranged living forms on a linear scale based on degree of perfection, also called the *scala naturae* or great chain of being. For more than 2,000 years after Aristotle, the chain was understood to be static, meaning that organisms and their rankings did not change. But in the early nineteenth century Jean-Baptiste de Lamarck added an evolutionary component, so that organisms moved up the chain as they evolved. A half century later the Darwinian view challenged the ordering itself. Darwin saw evolution as a process of branching and divergence rather than linear ascent. But Darwin nevertheless recognized progress, writing famously in *On the Origin of Species* of "that vague yet ill-defined sentiment, felt by many paleontologists, that organisation on the whole has progressed" (Darwin 1859, 363).

In evolutionary discourse since Darwin, progress has been acknowledged by many evolutionists, but the idea has also come to be seen as troublesome, both philosophically and scientifically. It is widely recognized that intuitions on evolutionary progress have been contaminated by cultural influences. We have a tendency to read into the history of life the social and technological progress we think we see in human affairs. Also, progress is now recognized as having two independent components that are frequently conflated, a value-neutral claim that long-term directional change has occurred and a value claim that the trend has been for the better. Among contemporary evolutionists the existence of a long-term trend is widely accepted. Most would agree that something is increasing. But what, exactly? And increasing in what sense? Is it progress? If so, progress in what sense? These issues have not been resolved, but the modern discourse has enabled us at least to formulate them fairly clearly.

Discussions of evolutionary progress can be found in the works of biologists, paleontologists, philosophers, and historians, including Thomas Huxley (1893), Herbert Spencer (1857), Julian Huxley (1942), Thomas Goudge (1961), Ledyard Stebbins (1969), Ernst Mayr (1988), George Gaylord Simpson (1949), Stephen Jay Gould (1988), Francisco Ayala (1974), Leigh Van Valen (1973), Geerat Vermeij (1987), Robert Richards (1992), Michael Ruse (1996), and others. Interestingly, among the scientists most of the discussion has been relegated to popular works. Ruse argues that the notion of progress has remained central in evolutionary studies, often its proof the chief motivating factor behind the work that people do, but that in the second half of the twentieth century the increasing professionalization of the field forced discussion of this value-laden subject out of the technical literature.

PROGRESS IN WHAT SENSE?

There are two ways in which a trend in some feature of organisms might have value. The feature could be valuable to us, or it could be valued by the evolutionary process, so to speak, in the sense of being preserved.

From a scientific standpoint the first alternative is problematic. In science our personal or cultural (religious, social) values should not be relevant or at least not central. Indeed, they are a distraction. For example, if the actual defining directionality in evolution were increasing energy usage, an infatuation with some feature we value, such as intelligence, might cause us to overlook it. Of course, we might be interested in the evolutionary sources of our values rather than trends generally. For example, it might be that intelligence is favored in evolution by natural selection, that we are the product of that trend, and that we value intelligence on account of its advantages for us. But here too the evaluative component of our interest is beside the point, except as original motivation. Thus it is hard to see how progress, if it is defined as a trend in features valuable to us, could be a scientifically useful notion.

The second alternative is to interpret valuable to mean that which is preserved, or, because we are interested in trends, that which increases over time. Progress then becomes a purely scientific term, but now doubts arise about the aptness of the word. It might be apt if the evolutionary process preserves features that strike us as positive, like intelligence, fitness, or complexity. But suppose we discover that the main long-term trend is an increase in a feature about which we are ambivalent, like energy usage, or a feature that seems downright bad, like fragility (leading to an increasing probability of extinction). It would sound odd to call either of these progress.

I think that these problems are fatal, and we should abandon talk of evolutionary progress and instead devote our energies to the study of trends. But the notion of progress has great cultural momentum and seems likely to persist, at least outside the technical literature, for some time to come. In what follows, I accede to the follies of my time and use the word *progress,* but only in the second sense, to mean that which is preserved. For convenience, I will also use the phrase *degree of advancement,* as though the variables involved in progress were either known or measurable. (As will be seen, at present they are not.)

A TREND IN WHAT SENSE?

Discussion of progress has been muddled, even recently, by confusion about how trends in groups work. In current trend theory it is not enough to say that some variable increases. To be clear, one must specify which of several group statistics is increasing—mean, maximum, or minimum—because trends in the different statistics have different interpretations. A trend in the mean is an increase in the average degree of advancement among all species in existence at a given time. Figure 1A shows a hypothetical long-term trend. Life begins with a single species, a single lineage, with some low level of advancement. As time passes, new species arise, and some species become extinct, with change occurring in the origin of every new species. The mean at any given time slice is the average level of advancement of all species in existence at that time. A trend is an increase in that average, that is, movement of the average to the right. A claim that a trend has occurred, without any qualifier, usually means an increase in the mean.

A trend in the maximum is a rise in the degree of advancement achieved by the most advanced species at a given time, in other words, a rise in the highest level of advancement achieved. (Figure 1B is the same as Figure 1A, but annotated to show the trend in the maximum, the dotted line on the right.) Maxima are of special interest because humans are generally thought to represent the most progressive species in existence and, if so, would represent the maximum in a time slice that included the present. We would be the last species on the right at the very top of the graph. Finally, a trend in the minimum is an increase in the degree of advancement of the least advanced species (the dotted line on the left in Figure 1B). Minima are of special interest because apparently the lowest level of advancement has not changed. Bacteria have existed, and indeed have dominated the biosphere, throughout the history of life.

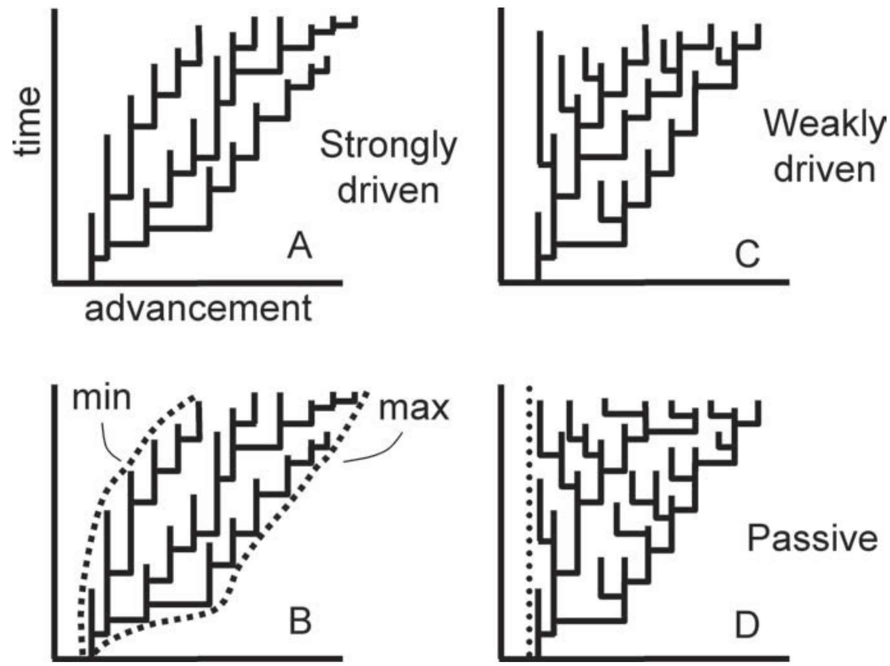

Figure 1. (A) A hypothetical long-term trend in advancement, that is, progress. Life begins with a single species, with some low level of advancement (the single vertical black line segment at the bottom left). As time passes, new species arise, and some species become extinct, with change occurring in the origin of every new species. Here all changes are increases, so the trend is said to be strongly driven. (B) Same as A, with dotted lines added to show the trends in the maximum and minimum. (C) A weakly driven trend in which increases predominate, but a number of decreases also occur. (D) A passive trend in which increases and decreases are equally frequent, but a lower limit on change (the vertical dotted line) forces lineages to diffuse to the right. See text for discussion.

Discussion of progress has not been concerned with the existence of a trend, perhaps because a trend is taken for granted (despite our inability to measure it). Rather, it has been about the pattern of change, the underlying mechanism. In Figure 1A natural selection strongly favors advancement, so that all changes are increases. The mean, maximum, and minimum all increase. Figure 1C is the same except that the net selective advantage is weak, meaning that selection sometimes favors decreases. (The classic examples are the evolution of certain reduced forms, like parasites.) The result is that less advanced species persist or are replaced by decreases from above, and the minimum stays roughly the same. The trends in 1A and 1C are said to be *driven,* or more precisely, 1A is strongly driven, whereas 1C is weakly driven. Figure 1D is different in that there is no overall selective advantage to increase. Increases and decreases occur equally often, so the only tendency is to spread symmetrically, both up and down. However, there is a boundary, a lower limit on degree of advancement, that blocks the spread of the group on the left. This boundary can thought of as the lowest level of advancement consistent with being alive. The result is that the mean and maximum increase while the minimum stays the same (as in the weakly driven case). The trend is said to be *passive*.

The current controversy over mechanism began in 1996 with a book on progress by Stephen Jay Gould in which he raised the passive mechanism to the level of plausibility. At issue is the role of selection in progress, that is, whether the (presumed) trend in the history of life is weakly driven by selection or merely passive. (A strongly driven mechanism is ruled out because the true minimum is thought to have remained stable: bacteria persist.) Gould has been widely misinterpreted as claiming that evolution is random, but the implication of the passive mechanism is not randomness. Within each evolving lineage selection does operate, and organisms are adapting. Rather, the implication is that evolving lineages as a group are governed by many different selective forces, complexly configured, so that selection favors increases and decreases equally often. The process can be understood as purely deterministic, like the diffusion of a gas.

Unfortunately, as will be seen, there are hardly any data available, so from a scientific perspective the debate about mechanism is taking place in a near vacuum. Still, theory has produced some insights. For example, it is now clear that in the debate over mechanism two common observations are irrelevant. The first is the persistence of nonprogressive species, the stable minimum. This observation is not helpful because the minimum is predicted to remain unchanged in both cases, passive and weakly driven. Likewise, the rise in the maximum and the current existence of some highly advanced species, like humans, are not helpful. A rising maximum is expected in all cases.

A TREND IN WHAT?

Many candidates for a long-term trend have been proposed: (1) fitness, (2) complexity, (3) ability to sense, control, or respond to the environment; (4) body size, (5) intelligence, (6) versatility or evolvability, meaning the ability to change in evolution, (7) the reverse of evolvability, also called degree of entrenchment, (8) energy intensiveness or rate of energy usage, and (9) depth and sophistication of mechanisms of inheritance. For the most part advocates of all these candidates have taken a case-building approach, with the result that the literature offers a number of clever and sometimes-powerful arguments in favor of each. Unfortunately, some of the most interesting—like fitness, complexity, energy intensiveness, and ability to control the environment—are difficult to operationalize. Thus there are hardly any data on the scale of life as a whole, for any trend statistic, for any of these candidate variables.

For some of these variables, many would want to count a long-term trend, if one could be documented, as progress. One variable is fitness, understood as ability to survive and reproduce. It might seem that Darwin's principle of natural selection virtually guarantees a trend in fitness. Later organisms should be more fit than earlier ones, on the whole, having beaten them, in Darwin's terms, "in the race for life" (Darwin 1859, 363). But as Darwin also knew, natural selection produces adaptation to local environments, and on geological timescales these change dramatically. Thus selection might produce just constant change with no net improvement, no net increase in fitness. On the other hand, on long timescales organisms with general adaptations, suiting them to a wider variety of environments, could be favored over those more narrowly adapted. Are there general adaptations that offer advantages on timescales of hundreds of millions or billions of years? There are some biological mechanisms that may have persisted that long, such as certain cellular transport mechanisms and parts of certain metabolic pathways. But we do not know how to identify general adaptations in any rigorous way, or how to test whether they have become more prevalent. All that is clear now is that both alternatives, a long-term trend and its absence, are possible in principle, and therefore this is an empirical issue.

The most widely recognized candidate for a long-term trend is complexity. As a possible basis for progress it is really a stealth candidate because a direct connection with progress is rarely acknowledged. But the way complexity is used in evolutionary studies suggests that it functions as a kind of code word for progress, superficially value free and therefore scientific sounding but still subtly connoting advancement. The absence of a widely known technical definition makes this usage problematic. Nobody knows what complexity is, so one can say anything at all about it. The literature of recent decades does contain a technical definition, or rather several definitions for each of the several senses of complexity. These include complexity in the sense of number of part types, number of physiological or behavioral processes, and number of steps in development (see Figure 2). However, little empirical work has been done, and with one exception, no trend that spans the history of life has yet been documented. Nor do we know very much about the mechanisms involved in change in these variables, passive versus driven. (On a smaller scale there is some evidence within the animals, over the past 500 million years, that there has been a trend in number of part types and that it has been passive.)

The exception is complexity in the sense of nestedness. Organisms are nested, to some extent, like Chinese boxes, with multiple levels of parts within wholes. Over the history of life, organisms with ever greater numbers of levels have evolved. The first living things 3.5 billion years ago were bacteria. About 2 billion years ago some bacteria joined together in a symbiotic relationship to produce the first eukaryotic cells, similar to modern protozoans such as *Amoeba*. They were superficially similar to bacterial cells, but because they evolved as colonies of bacteria, they occupied the next level up. Then about 600 million years ago clones of eukaryotic cells joined to produce the first multicellular individual (probably a kind of algae), the ancestor of all modern multicellulars, from mushrooms to magnolias to muskrats. Finally, about 480 million years ago clones of multicellular individuals joined to form the first colonial animal, a coral-like animal called a bryozoan. Modern colonial organisms include bryozoans, corals,

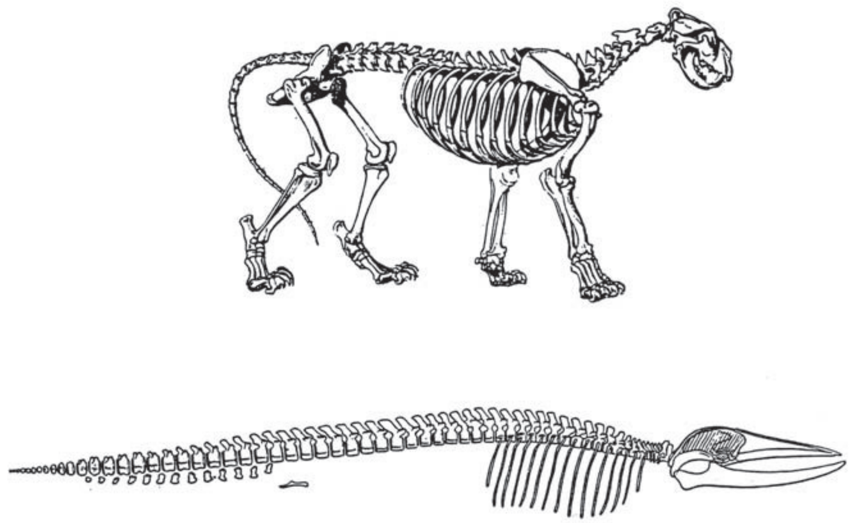

Figure 2. A classic example of why definitions of progress in terms of moves to complexity are problematic. The upper skeleton is of a lion and the lower skeleton is of a whale. By any measurement the backbone of the whale is the simpler, and yet adaptively the whale's backbone is what is needed for a marine mammal, just as the lion's backbone is what is needed for a terrestrial predator. Whales descended from land tetrapods (four-legged animals) and ~~so its backbone~~ marks a selection-driven move from complexity to simplicity. (From McShea 1991, 315.)

the social insects, and many vertebrates, from fish to humans. We do not know if even higher levels—colonies of colonies—have been reached. There are no clear-cut cases. Humans seem to associate at many levels, but only weakly at the higher ones. Interestingly, if humans have not truly reached the colony-of-colonies level, and if no other organism has either, this raises a novel possibility: the only variable in which we can document a trend, complexity in the sense of nestedness, in fact does show a trend, but that trend might have ended, perhaps 480 million years ago. Perhaps the age of progress is over.

BIBLIOGRAPHY

Ayala, F. J. 1974. The concept of biological progress. In F. J. Ayala and T. Dobzhansky, eds., *Studies in the Philosophy of Biology,* 339–354. London: Macmillan.

Goudge, T. A. 1961. *The Ascent of Life*. Toronto: University of Toronto Press.

Gould, S. J. 1988. On replacing the idea of progress with an operational notion of directionality. In M. H. Nitecki, ed., *Evolutionary Progress,* 319–338. Chicago: University of Chicago Press.

———. 1996. *Full House: The Spread of Excellence from Plato to Darwin.* New York: Harmony Books.

Huxley, J. S. 1942. *Evolution: The Modern Synthesis*. London: Allen and Unwin.

Huxley, T. H. 1893. *Evolution and Ethics*. London: Macmillan.

Mayr, E. 1988. *Toward a New Philosophy of Biology: Observations of an Evolutionist*. Cambridge, MA: Belknap Press of Harvard University Press.

McShea, D. W. 1998. Possible largest-scale trends in organismal evolution: Eight "live hypotheses." *Annual Review of Ecology and Systematics* 29: 293–318.

———. 1991. Complexity and evolution: What everybody knows. *Biology and Philosophy* 6, no. 3: 303–325.

Richards, R. J. 1992. *The Meaning of Evolution: The Morphological Construction and Ideological Reconstruction of Darwin's Theory*. Chicago: University of Chicago Press.

Ruse, M. 1996. *Monad to Man: The Concept of Progress in Evolutionary Biology*. Cambridge, MA: Harvard University Press.

Simpson, G. G. 1949. *The Meaning of Evolution*. New Haven, CT: Yale University Press.

Spencer, H. 1857. Progress: Its law and cause. *Westminster Review* 67: 244–267.

Stebbins, G. L. 1969. *The Basis of Progressive Evolution*. Chapel Hill: University of North Carolina Press.

Van Valen, L. 1973. A new evolutionary law. *Evolutionary Theory* 1: 1–30.

Vermeij, G. J. 1987. *Evolution and Escalation*. Princeton, NJ: Princeton University Press.

—D.W.M.

Evolutionary Psychology

Some behavioral scientists define evolutionary psychology as simply the study of human behavior and psychology from an evolutionary perspective. In this broad sense, evolutionary psychology is a field of inquiry. Fields of inquiry are defined not by specific theories about the phenomena they study, but by the kinds of questions they pose about them. Fields of inquiry thus differ from paradigms, which are defined by the specific theories and methodologies with which they answer the questions that define a field of inquiry. As a field of inquiry, evolutionary psychology began with Charles Darwin's publication of *The Descent of Man* in 1871 and *The Expression of the Emotions in Man and Animals* in 1872. It was not until a century later that clearly articulated paradigms began to emerge in evolutionary psychology, each with distinct theories about, and specific methods for studying, the evolution of human behavior and mentality.

The first of these paradigms was human sociobiology, which emerged in the 1970s. The core idea of sociobiology was that behavior has evolved under natural and sexual selection just as organic form has. For example, females of many species choose mates based on the quality of male courtship displays. If male courtship displays vary in quality, and that variation is heritable, sexual selection will tailor male courtship behavior to female preference. In this way, sociobiologists argued, a form of behavior can be an adaptation, whose presence in a population is to be explained by the principles of evolutionary theory. Accordingly, human sociobiology sought to offer evolutionary explanations of how humans are behaviorally adapted to social life with one another—to explain human behavioral adaptations for dominance hierarchies, for manifesting and dealing with aggression, and for mating. Indeed, the central theoretical problem of human sociobiology was to explain the