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# Evolutionary Progress?

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BY TIMOTHY SHANAHAN

*Progress might have been all right once, but it has gone on too long.* (Ogden Nash 1962, p. 11)

That the history of life on Earth manifests some sort of progress has seemed obvious to many biologists. Once there were only the simplest sorts of living things—replicating molecules, perhaps. Now the world contains innumerable species displaying amazing adaptations fitting them for every conceivable niche in the economy of nature. How could anyone who accepts an evolutionary view of life deny that progress has occurred? Yet perhaps no other issue in evolutionary biology has inspired such passionate controversy. According to one prominent critic, Stephen Jay Gould, "Progress is a noxious, culturally embedded, untestable, nonoperational, intractable idea that must be replaced if we wish to understand the patterns of history" (Gould 1988, p. 319). Other critics, such as William Provine, are somewhat less contemptuous but equally dismissive of the idea of evolutionary progress, issuing the common complaint that "the problem is that there is no ultimate basis in the evolutionary process from which to judge true progress" (Provine 1988, p. 63).

Undaunted by these attacks, however, contemporary friends of the concept of evolutionary progress have insisted on its centrality in a Darwinian view of life. According to Richard Dawkins, the most important features of evolution simply cannot be understood correctly without embracing the notion of evolutionary progress: "[A]daptive evolution is not just incidentally progressive, it is deeply, dyed-in-the-wool, indispensably progressive. It is fundamentally necessary that it should be progressive if Darwinian natural selection is to perform the explanatory role in our world view that we require of it, and that it alone can perform" (Dawkins 1997, p. 1017). In Ernst Mayr's view, progress in evolution is simply as obvious, and as undeniable, as the manifest progress in the development of the automobile (Mayr 1994).

As these divergent viewpoints reveal, the notion of evolutionary progress remains a hotly contested idea in evolutionary biology (Gould 1996, 1997, Ruse 1996). A cursory examination of this issue might tempt one to conclude that it is inherently unresolvable (Ruse 1993). But as I will try to show, the question, "Is evolution progressive?" admits of the same sort of answer as other questions in evolutionary biology. The key lies in spelling out more carefully the meaning of the term evolutionary progress. But although being clear about the meaning(s) of this term is necessary, it is not sufficient for answering this question. Once the meaning(s) of the term evolutionary progress has been clarified, there remains the empirical and interpretive task of determining whether evolution is progressive in one or more of these senses.

There are, then, two basic questions concerning evolutionary progress: First, what is meant by evolutionary progress? Second, is evolution, in fact, progressive? With regard to the first question, I will argue that the notion of evolutionary progress has both a core meaning as well as a set of clearly specifiable alternative interpretations, each of which needs to be carefully identified. In response to the second question, I will argue that if some conceptions of evolutionary progress are exemplified in the history of life, then evolution must be considered progressive, at least insofar as those conceptions are concerned. Indeed, given the range of legitimate interpretations of evolutionary progress, it will almost necessarily be the case that evolution is progressive according to one of these interpretations.

## What is evolutionary progress?

The notion of evolutionary progress has accumulated a range of connotations. Consequently, it is worthwhile to return to the core concept of evolutionary progress (i.e., those features of evolutionary progress that virtually everyone, despite their other differences, would agree to) to see what the basic concept requires. This can be done by imagining a hypothetical world in which there is no evolutionary progress and then adding elements to this picture one by one until progress emerges. The result will be the minimum set of ingredients necessary for evolutionary progress.

***Evolutionary progress requires change in a population.*** Imagine a world of entities in which there is no change whatsoever. An observer visiting that world today would observe exactly the same things as she would have seen on a visit a hundred, a thousand, or a million years ago. Clearly, such a world would not be described as

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embodying progress in any form. Without change, there can be no progress. But mere change is not sufficient. Simply altering the relative positions of the entities in that world, for example, or modifying the individual entities themselves would entail change but not evolutionary progress, because evolutionary progress requires a change in the ensemble of the constituents of a world through addition to or replacement of its previous constituents. There must be a population of entities whose membership changes over time. Even this change is not sufficient, however, because one can imagine a world in which the membership in the set of entities populating that world changes over time, but because the replacements are qualitatively identical to those replaced there has been no evolutionary change. A visitor returning to such a world after a year's absence would not notice any difference. Evolutionary progress requires sequential change in the relative frequencies of the properties characterizing a population of entities, such that the frequency of any given property changes over time.

***Progressive evolution has a direction.*** Returning to our hypothetical world, suppose, next, that the sort of changes just described occur. Would such a world now necessarily embody "progress"? Clearly not, because the changes could be purely random: The relative frequencies of the properties characterizing a population of entities might change in a haphazard fashion, without any discernible pattern. Simply making the changes nonrandom would likewise be insufficient to produce evolutionary progress. If the properties of the entities of this hypothetical world were to change in a cyclical fashion, such that the same properties appeared, disappeared, and then reappeared with monotonous regularity (like waves crashing on the beach), then, even though a nonrandom pattern would be present, there would be no evolutionary progress. Evolutionary progress presupposes not only sequential change and patterns but also significant trends. There has to be some discernible direction to the changes taking place to make a claim for evolutionary progress even remotely plausible.

***Progressive evolution is gradual.*** But is directional change sufficient for evolutionary progress? No, because not every directional change can be properly described as evolutionary. If the properties of an object change abruptly, or if one thing is simply replaced by another, different thing, this would not be an evolutionary change. Evolution, by definition, is a step-by-step transformation. If I trade in my rusty old gas-guzzling jalopy for a new, fuel-efficient automobile, there has been a directional change but not an evolutionary change because no series of intermediates connects the two cars. On the other hand, if an automobile manufacturer introduces new features on the same model of car year after year, each time using the previous year's version as the starting point for the new design features, this would be a directional evolutionary change.

***Progressive evolution manifests improvement.*** Let the entities in the imaginary world undergo gradual directional change. Does this form of change constitute progress? Not necessarily. The notion of progress is inherently value laden in a way that directionality is not. If a set of objects gradually becomes pinker over time, we might describe them as having become progressively pinker. But unless it is "better" for these objects to be pinker, this gradual directional change cannot be considered progress. Likewise, we might say of someone's terminal illness that it has progressed to such a state that further treatment would be futile—but the patient would hardly think of his imminent demise as progress. Clearly, some improvement must occur for gradual directional change to count as evolutionary progress.

***Evolutionary progress is gradual directional change embodying improvement.*** Taking these considerations together, the basic ingredients of evolutionary progress are change, direction, gradualism, and improvement. These requirements are individually necessary and jointly sufficient for evolutionary progress. Any world in which objects are undergoing gradual directional change embodying improvement would be a world in which there is evolutionary progress (Ayala 1988).

## Is "improvement" a scientifically respectable concept?

Although the ideas of directionality and gradualism are more problematic than they might at first seem, both can be given plausible operationalist definitions (Dawkins 1992). Not surprisingly, the idea of improvement poses the most problems because it seems to introduce values into an otherwise objective, value-free intellectual enterprise. According to one venerable view, science eschews all value judgments in favor of identifying facts (empirical data), establishing their interconnections (laws of nature), and then explaining the interconnections (theories). Assessments of good or bad are kept strictly at arm's length and are vigilantly prevented from intruding into the epistemic purity of scientific investigation.

It is hardly necessary to point out how misleading this view of science is. The idea of improvement is indeed value laden, but then so is all good science. Some values are simply inherent in science as an intellectual enterprise. For example, scientists value theories that are simple, explanatory, predictive, wide in scope, empirically confirmed, and consistent with findings in other areas of science. Based on such standards, scientists routinely and without apology judge one theory to be better than another (e.g., general relativity versus Newtonian mechanics; descent with modification versus special creation) because one of the theories better satisfies the standards they value. A given scientific theory is deemed good relative to some set of standards that is intrinsic to the scientific enterprise, and some theories are judged to be better than, and an improvement over, others. Such assessments are thoroughly value laden.

"Good" in the context of assessing scientific theories is a term of epistemic appraisal. Additional nonepistemic values are part and parcel of evolutionary biology. A particular property of an organism might be described as good for achieving a certain result (e.g., capturing prey, evading a predator, sensing the environment). For any characteristic of an organism, it makes sense to ask what it is good for (although there is no guarantee that every characteristic of every organism is good for something, nor that every good characteristic requires an evolutionary explanation). Good, in this context, typically refers to some kind of functional efficiency. A given characteristic might be described as good if it contributes to the solution of a problem facing the organism in its particular environment. Again, some characteristics might be better at solving a particular problem than others, and a transition to this better characteristic represents a biological improvement. Consequently, the idea of improvement scientifically is not only respectable but also essential to science as an intellectual activity responsible to certain epistemic values and to evolutionary biology as the pursuit of causal explanations for the functional characteristics of living things (Sober 1994).

## Alternative standards of evolutionary progress

Common to the value judgments inherent in both the scientific enterprise and in evolutionary biology is the idea that something can be judged good, and perhaps better than something else, relative to a given standard. Claiming that evolutionary progress entails improvement relative to some standard is one thing; specifying that standard is quite another. Accordingly, the central problem in determining whether evolution manifests progress concerns the identification and justification of a standard according to which improvement can be measured. As might be expected, much of the debate over evolutionary progress has focused on this problem.

***Absolute versus relative progress.*** According to some discussions of evolutionary progress, it is essential to ask whether the standard of improvement is absolute or relative (or comparative). For example, according to Ruse (1993), absolute progress involves "the climb up some objective scale," whereas comparative progress involves "competition between groups" (Ruse 1993). This way of characterizing the distinction between absolute and relative progress is clearly inadequate. Even if there is some objective scale that organisms or species may be said to climb, it would still be true that any judgment that organisms or species had progressed would have to be made relative to this particular scale. Likewise, to say that comparative progress involves competition between groups presupposes some standard that is independent of both groups, according to which one group can be judged competitively superior to another. Either way, progress can be judged only in relation to some standard.

How, then, should the distinction between absolute and relative progress be made? On one hand, the standard by which evolution is judged to be progressive might be independent of context, space, time, or biological factors—that is, the standard or goal may represent some fundamental value that transcends the particular details of the history of life on Earth, a value that is inherent in reality (e.g., a Platonic Form) or in the mind of God. Pierre Teilhard de Chardin's cosmic evolutionism culminating in "The Omega Point" (the predetermined final goal of all creation) might be an example of progressionist thinking that presupposes an absolute standard of evolutionary progress in this sense (Teilhard de Chardin 1959), although even here progress is measured relative to some standard. On the other hand, the standard(s) by which evolution is judged to be progressive might depend on strictly biologically relevant criteria, for example, on the functional characteristics of living things themselves in relation to their environments. Possible examples of relative progress according to this type of standard include the emergence of multicellularity and the division of physiological labor, of homeothermy, of sociality, and of efficient terrestrial locomotion, all of which can be seen as having improved the functional performance of the living things in question.

Although the belief that there is just one standard by which evolutionary progress must be judged is not a formal entailment of the notion of absolute progress, it is nonetheless often connected with it. By contrast, proponents of the notion of relative progress typically leave open the possibility of there being more than one standard by which evolution might be judged to be progressive. Critics of the idea of evolutionary progress often just assume that any progress worth talking about must be progress in the absolute sense, and so easily dismiss the idea of evolutionary progress as mystical nonsense (Provine 1988). On the other hand, those friendly to the idea of evolutionary progress typically endorse some kind of relative progress (Ayala 1988). Because the idea of absolute progress is endorsed by few if any evolutionary biologists and is consequently not an issue figuring in current debates about evolutionary progress, I will focus exclusively on the possible meanings of relative progress (henceforth referred to simply as progress).

***Natural facts and artificial constructs as alternative types of standards.*** Evolutionary progress presupposes some standard in terms of which improvement could, in principle, be measured. There are, however, two bases upon which standards of measurement can be established: natural facts and artificial constructs. Natural facts exist independent of any act of human creativity. For example, atomic weight and, more generally, the properties displayed on the periodic table represent natural facts about the basic elements. Likewise, the distance that light travels in a year is a natural fact represented in the light-year as a unit of measurement. A standard of evolutionary progress represents a natural fact if evolution is progressive (or not) independent of human concerns, questions, or investigations. Evolutionary progress might thus be a natural fact in the same way that we typically think of natural laws, forces, fields, particles, atomic weights, the speed of light, DNA, organisms, or populations as being objectively real whether or not anyone studies these things, cares about them, or even knows of them.

If evolutionary progress is a natural fact, then it is perfectly possible for there to be evolutionary progress even though we are unable to measure (and hence demonstrate) it. Consider again the analogy with fundamental particles. If there are fundamental particles (the constituents of quarks, perhaps), then this is a fact about nature that is true independent of human observers, and it is conceivable that we will never discover these particles or their exact properties, either because of their nature or because of ours. Similarly, suppose that evolutionary progress consists of an increase in some property of organisms, but that we are either ignorant of this fact or unable to accurately measure this property. In this case, there might be evolutionary progress, even though it is not possible to show that there is.

Thus, unless one adopts an operationalist definition of progress, according to which the very meaning of progress is determined by the procedures that are used to measure it, it will always remain possible that evolutionary progress exists but eludes our ability to observe it. This possibility is not nearly as odd as it might seem. After all, presumably it either is or is not the case that there is a series of five consecutive twos in the decimal expansion of pi, even though we may never know which of these possibilities is correct. Likewise, there either are or are not intelligent aliens inhabiting other worlds, even though we may never find out that there are (or are not). Such claims are merely applications of the philosophical view known as scientific realism: Nature exists independent of us and need not be coextensive with our abilities to know it. Reality, according to the realist, should not be conflated with knowability. Incidentally, this was a point about which Darwin himself, writing in *On the Origin of Species*, was quite clear: "I do not doubt that [a] process of improvement has affected in a marked and sensible manner the organisation of the more recent and victorious forms of life, in comparison with the ancient and beaten forms; but I can see no way of testing this sort of progress" (Darwin 1959, p. 337). In summary, being unable to identify or measure evolutionary progress does not mean that evolutionary progress is unreal, any more than being unable to identify or measure sub-quarkian fundamental particles shows that such particles are unreal.

To say that a standard is an artificial construct is, by contrast, to say that it is invented by us to pick out properties of things of interest to us. For example, the concept of a meter picks out a real property of physical objects—their length—but, although this concept is clearly useful, it is not supposed to "carve nature at its joints" (to borrow a phrase from Plato) or to represent a natural kind that would automatically be recognized by, say, extraterrestrial scientists. Although some objects were precisely *X* meters long for eons before humans arrived on the scene, and at least some of them will continue to be the same length long after humans as a species have departed, it is only by virtue of our interests and concerns that the fact of something being any number of meters long has any significance. We did not invent all of the objects that we measure with the metric system, nor did we invent length—but we did invent the metric system itself, by which the length of objects is measured. It is worth stressing that the properties a constructed standard picks out may well be perfectly real. That is, a meter picks out a real property of objects, even though the unit of measurement itself is invented by humans for our purposes. A constructed standard can pick out imaginary properties of natural objects as well, although these will usually be of much less interest to those who wish to understand the natural world.

To say that a standard of evolutionary progress is an artificial construct is, thus, just to say that it has been invented to serve our concerns, our questions, or our quest for understanding, and that apart from us (or other creatures capable of considering the issue) there is no fact of the matter about whether evolution is or is not progressive. Notice that despite its invented character, a constructed standard of evolutionary progress might nonetheless pick out real properties of organisms or evolving lineages and thus tell us something both interesting and true about the evolutionary process. There might, of course, be more than one constructed standard of evolutionary progress, with the consequence that specific aspects of the evolutionary process might be judged progressive according to one standard but not according to another.

Surprisingly, evolutionary progress as measured by a constructed standard is in exactly the same epistemological boat as the notion of evolutionary progress as a natural fact. That is, it is possible that we are unable to know that evolution is progressive or to properly measure its progressiveness, even though we ourselves invented the standard of evolutionary progress. This inability may seem paradoxical at first. As a conceptual invention, a constructed standard is known as soon as it is formulated. But knowing what the standard requires and knowing precisely how it applies in a given situation are two different issues. The constructed standard may be crystal clear, but its application in a particular instance might be completely murky. Consider an analogy: The nanometer as a unit of measurement is perfectly clear, but it might be impossible to determine how many nanometers in diameter a given object is because the object is too small, is too large, is constantly moving, or is hidden inside other structures. Likewise, someone might propose increasing complexity as a standard of evolutionary progress and devise a rigorous definition of complexity, but be unable to accurately measure the complexity of a given biological entity. Consequently, even if a given standard of evolutionary progress is constructed, there is no guarantee that we can know whether evolution is progressive or not according to this standard.

## The modalities of evolutionary progress

The foregoing distinctions and clarifications are essential to understanding as clearly as possible both the core idea of evolutionary progress and the different kinds of standards that can be used to measure evolutionary progress. To bring the issue of evolutionary progress into sharper focus, additional distinctions are necessary concerning the pervasiveness of evolutionary progress, the property or properties that might increase in evolution, and the identification of the entities that might undergo progressive evolutionary change. Each distinction centers on a controversial issue in contemporary discussions of evolutionary progress.

### *Universal versus episodic evolutionary progress.*

One of these issues is whether evolutionary progress, if it exists at all, is universal or merely episodic. Evolutionary progress is universal if evolution is everywhere and at all times manifesting progress. Evolutionary progress is episodic if evolution is at least sometimes, for some lineages, progressive. Episodic evolutionary progress is compatible with both periods of stasis, in which no progress occurs, and periods of regression, in which some lineages revert to an earlier form. Clearly, evolution might be episodically progressive without being universally progressive, but not the converse.

Few evolutionary biologists argue that evolution is always and everywhere progressive because, among other reasons, there appears to be no single standard according to which universal evolutionary progress may be judged to have occurred. For example, complexity, size, or perceptual abilities increase in some lineages and decrease in others and sometimes change direction even within a given lineage. Saying that evolution is episodically progressive, however, leaves open a number of distinct possibilities that range from saying that there is at least one instance of evolutionary progress—no matter how local and fleeting—in the history of life, to saying that evolution is occasionally progressive, to saying that evolution is often progressive, to saying that it is usually (in a majority of lineages for most times) progressive, to saying that evolution is almost always (but not quite universally) progressive. Because the issues of what proportion of lineages manifest progress and of how long any given lineage manifests progress are distinct, the assertion that evolution is (episodically) progressive could result in a number of distinct theses. For example, evolution might be progressive in all lineages over all time periods (i.e., universally progressive), progressive in all lineages over some but not all time periods, or always progressive in some but not in all lineages. Simply asserting (or denying) that evolution is progressive does not make clear which of these distinct theses is meant. Being clear about the extent of the evolutionary progress one is considering is essential for answering the question, is evolution progressive?

### *Uniform, net, and apex evolutionary progress.*

Ayala (1988) makes a related but different distinction between uniform and net progress: "*Uniform progress* takes place whenever every later member of the sequence is better than every earlier member of the sequence according to a certain feature.... *Net progress*...requires only that later members of the sequence be better, *on the average*, than earlier members" (Ayala 1988, p. 79). Clearly, these forms of progress are not mutually exclusive. If uniform progress occurs, then by definition so does net progress, although the converse is not necessarily true.

Ayala's distinction is useful, but to understand the idea of evolutionary progress as clearly as possible it is necessary to make a further distinction. Imagine a case in which the evolutionary change in a given sequence has been nonuniform, such that even though later members of the sequence are not on the average better than earlier members, something has occurred that can reasonably be regarded as evolutionary progress. For example, consider intelligence (and suppose for the moment that this is a well-defined concept). In addition, suppose that it is possible to rank] organisms on a scale from 1 to 10 with regard to their intelligence, with organisms at level 1 being exceedingly stupid and organisms at higher levels being increasingly more intelligent. Finally, suppose that at time T1 there are organisms at level 4 but no higher, whereas at some later time, T2, there are organisms at level 7. In this case, the upper level of intelligence would have increased. But this increase in the upper intelligence level could have occurred even if the average intelligence level dropped or if the sequence leading up to it changed in a nonuniform fashion. For example, the organisms occupying lower levels of the intelligence scale might be far more numerous than those occupying the higher levels, or the number of individuals within species at the lower levels might far outnumber those occupying the higher levels, dragging the average level of intelligence down. Conversely, the average level of intelligence could increase without a corresponding increase in the highest level of intelligence achieved (e.g., if the number of entities at an intermediate level of intelligence increases relative to the number of entities at lower levels).

Consequently, there are at least three alternative meanings to the claim that the history of life manifests progress. This claim might mean that with respect to some property, every individual later in a sequence is an improvement upon all those that preceded it (uniform progress); that later members of the sequence are, on average, better than those that came before (net progress); or that some (but not necessarily every) later member of the sequence is better than every earlier member of the sequence according to a certain feature (apex progress).

It is, in fact, this last conception of evolutionary progress—namely, that higher levels of a certain property or characteristic appeared later in the history of life than lower levels—that generally first comes to mind when considering the idea that life has advanced from its simple beginnings. If one considers mammals to be higher than insects, and if mammals appeared later in the history of life than insects, then according to this conception evolution has manifested progress. Likewise, if there are currently organisms with greater intelligence than any that came before, then there has been evolutionary progress with regard to intelligence. This conclusion would be valid even if, as seems to be the case, such intelligent organisms constitute only a minuscule fraction of all living things (considered in terms of either species or number of individuals), now or in the past.

***Life, lineages, species, properties.*** Discussions of evolutionary progress are often marred by unclarity concerning the objects that are thought to manifest progress. One can speak of progress in the evolution of life (taken as a whole), within an evolutionary lineage (e.g., of horses), within a particular species (e.g., *Equus caballus*), or of distinct properties (e.g., efficient terrestrial locomotion). Clearly, it might be possible to find progress (in one of the senses defined earlier) in one or more of these objects but not in others. For example, progress within the horse lineage does not entail progress in life as a whole or even within a given species of horse. That is, within the horse lineage there might, over the course of several million years, be an increase in running speed, even though there is no increase in running speed within a given horse species, the average or maximum running speed of its members remaining constant throughout its existence. Such possibilities will be ever present when dealing with objects consisting of constituent parts or members. What is true of the whole need not be true of each part, and vice versa.

In like manner, there is no reason why progress must include improvement in every aspect of the organism under consideration. Use of the terms higher and lower with respect to organisms often seems to imply that organisms are higher or lower as a whole, rather than with respect to some particular property or set of properties. But because organisms can be thought of as clusters of properties, it is possible for organisms appearing later in a lineage to be "higher" than their predecessors in one respect but not another. For example, the fossil record might reveal a long-term trend toward increased size and reduction in the number of toes within the horse lineage—changes that might be judged improvements for efficient terrestrial locomotion. However, there may have been no corresponding changes or improvements in dentition in the lineage. Of course, although one organism may be judged as higher overall than another, especially within a given lineage, it may not always be possible to rank whole organisms in this fashion, especially when organisms in distinct lineages (e.g., beetles and barracuda) are being compared. Consequently, disagreements about evolutionary progress can probably be minimized (although not eliminated completely) by specifying as precisely as possible the property or set of properties at issue and the relevant comparison class (i.e., organisms in the same or in different lineages). Ultimately, what is important is not trying to determine the true object of evolutionary progress but rather being clear about what, precisely, a given claim of evolutionary progress is asserting and then conducting whatever investigation is necessary to determine whether that particular claim is true.

## The magnitude of evolutionary progress

In addition to the modalities of evolutionary progress, we can also consider, more briefly, its magnitude. Ruse (1993) locates the debate over evolutionary progress in two points: significant, new adaptations (innovations) and long-term trends. Evolutionary innovations are adaptive breakthroughs, adaptations that cross a functional threshold. Although explanations for the prevalence of innovations at certain times in the history of life vary (Nitecki 1990), they are seen by proponents of progress as embodying evolutionary progress in its most dramatic form. Despite their striking character, however, innovations are merely especially obvious instances of evolutionary improvement. A slight increase in the running speed of a predator is no less an evolutionary improvement than the development of wings for flight. Long-term trends may be the result of the slow accumulation of gradual improvements, of relatively rapidly appearing evolutionary innovations, or of both. It is important to recognize, however, that evolutionary progress can span the spectrum from slight, hardly noticeable improvements in some preexisting functional property of an organism right up to the dramatic changes associated with the appearance of entirely new structures and capacities. Differences in the magnitude of evolutionary improvement do not alter the essential nature of evolutionary progress, although they may make it more conspicuous.

## The causes of evolutionary progress

A basic distinction within evolutionary biology is between pattern and process. The former refers to a sequence of events in the history of life or of a particular lineage, for example as described in a phylogenetic tree. The latter refers to the events responsible for generating this pattern. Clearly, establishing that a particular pattern has occurred is one thing; explaining why this pattern exists by identifying its causes is another. In considering the causes of evolutionary progress, two additional sets of distinctions are important as well.

***Driven versus passive trends.*** An evolutionary trend might be either driven or passive (McShea 1994). A driven trend is, as its name suggests, one in which some force drives or pushes the evolution of the lineage in a particular direction. An example would be an evolutionary "arms race" between predator and prey. As each side becomes better adapted at capturing or escaping capture, respectively, the other side is forced to develop counteradaptations, resulting in, for example, increases in maximum running speed for both lineages (Dawkins and Krebs 1979). A passive trend is one in which no such force is operative but rather a lineage evolves in a certain direction, either because that is the only available evolutionary path or because evolution in one direction is less constrained than in other directions. For example, there might be a passive trend toward increasing complexity, not because complexity is better but just because if the organisms in a lineage begin as very simple creatures, they are more likely to evolve in one direction (e.g., toward increasing complexity) than the other (Maynard Smith 1988).

The distinction between driven and passive trends is reasonably clear to most biologists. The relationship between these two kinds of trends and evolutionary progress is less so. It is tempting to associate progressive evolution with driven trends and to conclude that passive trends cannot or do not manifest progress (e.g., Gould 1996). But a moment's reflection demonstrates that this neat picture is too simple.

First, one can imagine a driven trend that is nonprogressive. For example, consider a population consisting of both altruistic (e.g., non–resource-exploiting) and selfish (e.g., resource-exploiting) organisms, and suppose that selfish individuals are at a selective advantage relative to altruists. As the proportion of selfish organisms in the population increases, resources are depleted and every organism's fitness decreases. Such a population could, through the operation of natural selection, be driven to extinction. Although such an outcome is not inevitable, it is certainly possible and, if it occurred, would hardly be considered progressive.

Second, one can imagine a passive trend that is progressive. Suppose that, through genetic drift, a lineage evolves in the direction of increased resistance to a particular disease-producing microbe, to which the members of that lineage come into contact only after resistance has been established. Such a trend would be both passive and progressive. Clearly, therefore, a trend need not be driven for it to constitute an instance of evolutionary progress. The fundamental fact underlying these hypothetical cases is that evolutionary progress concerns the pattern of evolutionary change, not its causes. So long as there is gradual directional change embodying improvement, there is evolutionary progress, irrespective of the causes of the change.

***Necessary versus contingent evolutionary progress.*** Entirely passive progressive evolutionary trends are theoretically possible. However, the basic logic of the theory of natural selection suggests that most progressive trends involving refinements in adaptations will be driven by natural selection operating on evolving lineages. At times Darwin himself seems to suggest that evolutionary progress is a necessary and inevitable outcome of the operation of natural selection (e.g., Darwin 1959, p. 221). At other times he makes it clear that he rejects belief in "an innate and necessary law of development" in evolution. On the contrary, "the doctrine of natural selection or the survival of the fittest...implies that when variations or individual differences of a beneficial nature happen to arise, these will be preserved; but this will be effected only under certain favourable circumstances" (Darwin 1859, p. 169). Darwin saw clearly that, although natural selection remains the best explanation for progressive evolutionary trends, it does not guarantee such trends, nor are there any other evolutionary factors that would make evolutionary progress inevitable. Indeed, apart from simply defining evolution as progressive, it is difficult to see what could motivate or sustain the view that evolutionary progress is inevitable. Viewing evolutionary progress as contingent, that is, as dependent on the particularities of the process itself, including historically unique events, is consistent with the more generally contingent nature of evolution (Gould 1986).

## *Is evolution progressive?*

Stepping back now from the set of basic distinctions introduced above, it is clear that there are three general positions to consider when attempting to determine whether evolution is progressive: dogmatic evolutionary antiprogressionism (evolution is never progressive in any sense); dogmatic evolutionary progressionism (evolution is always and everywhere progressive); and modest evolutionary progressionism (evolution is at least sometimes, in precisely specified ways, properly described as progressive).

How plausible is each position? Given the wide variety of different conceptions of evolutionary progress, only the most obvious of which have been discussed above, dogmatic evolutionary antiprogressionism is very unlikely to be correct, if for no other reason than that there are so many ways in which it could be wrong. If there is even one sense in which evolution manifests some sort of progress, then dogmatic evolutionary antiprogressionism is refuted.

Dogmatic evolutionary progressionism is also unlikely to be correct, but for an entirely different reason—namely, that it is not even clear, except in a trivial sense, that evolution is always and everywhere anything. Biological systems are distinguished as much by their failure to conform to the general rules humans devise as by the rules themselves. Females make a greater investment in offspring in the form of parental care than do males—except when they don't (e.g., in sea horses). Offspring in sexually reproducing species are just as closely related to their parents as they are to their siblings—except when they aren't (e.g., in Hymenoptera with haplodiploidy). Bright, conspicuous colors indicate extreme toxicity—except when they don't (e.g., in harmless snakes that mimic poisonous coral snakes). It is such exceptions to the general rules that seem to distinguish the history of life on Earth from the subject matter of physics, in which apparent exceptions to the basic principles (e.g., the anomalous perihelion of Mercury in relation to Newton's laws) are rare and demand either a revision of the theory or its replacement by a more adequate theory. In evolutionary biology, on the other hand, we are intrigued, but hardly surprised, when we learn of some deviation from the normal patterns we have come to expect. Although we cannot always anticipate each particular biological novelty that appears, we nonetheless expect that there will be novelties of one sort or another. Darwin, of course, captured the distinction between the character of physics and biology beautifully in the final words of *On the Origin of Species*, in which he contrasted the earth, considered simply as another planet "cycling on according to the fixed law of gravity," with the grandeur of life on Earth, in which "endless forms most beautiful and most wonderful have been, and are being, evolved" (Darwin 1859, p. 490).

If both dogmatic evolutionary antiprogressionism and dogmatic evolutionary progressionism are inherently implausible doctrines, that leaves modest evolutionary progressionism. Given that there are so many different, legitimate ways to construe the claim that evolution is progressive, it is correspondingly likely that evolution is, at least sometimes and in some precisely specified way, properly described as progressive. Even more generally, in light of the core idea of evolutionary progress introduced earlier, the question of whether evolution is progressive is just the question of whether there have been any gradual directional changes in the history of life that embody improvement relative to some standard.

Clearly there are examples of such changes. Eyes have undergone progressive evolution from simple pinhole camera-type eyes to the complex eye of the hawk (Dawkins 1996). Wings have undergone progressive evolutionary improvement, from the proto-wings of archaeopteryx to the highly specialized wings of modern birds. Arguably, the four-chambered heart of mammals is an improvement over the three-chambered heart of reptiles and birds (Walker and Liem 1994). Homeothermy is conceivably an improvement over poikilothermy. It is even plausible (although currently an anathema among those vigilantly guarding the purity of the scientific enterprise from the dangers of anthropocentrism) to suppose that intelligence is an adaptation that serves some organisms quite well and that the sort of intelligence associated with human cognition has improved over evolutionary time, as evidenced by a directional trend in the hominid lineage toward greater brain volume.

None of these examples entails or suggests in any way that every property of organisms in every lineage has experienced continual improvement over every segment of its evolutionary history. Nor do they suggest that evolution as a whole is progressive. Those are distinct claims that can be assessed only by the daunting task of taking into account the full range of biological examples. What these examples do suggest is that there is a straightforward and unproblematic sense in which evolution is correctly described as progressive. Evolutionary progress is quite real, albeit probably more limited in both scope and significance than many advocates of evolutionary progress suppose.

## Conclusions

Progress, in one form or another, has been part of the evolutionary process from its beginning and is likely to remain so for as long as the process continues. Debates about evolutionary progress of the sort that have characterized discussions of this issue from Darwin to the present, however, are another matter. Ogden Nash's remark about progress should be reformulated for debates about evolutionary progress: The debate about evolutionary progress might have been all right once, but it has gone on too long. It is time for the debate over evolutionary progress to move beyond the simple question of whether evolution is progressive or not, to a more detailed investigation of the nature, causes, and extent of evolutionary progress.

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