

Evolution is opportunistic, not directional

In a recent article published in *BioScience*, Timothy Shanahan (2000) argues, among other things, that evolution is progressive, directional, and embodies improvement. However, empirical evidence from a vast array of organisms that display evolutionary loss of a number of phenotypic characters present in their ancestors contradicts such assertions. Furthermore, the use of vague terms reintroduced in Shanahan's article to define or describe evolution in lieu of standard terminology currently used in biology will result in confusion rather than in clarification of ideas.

A past example of what Shanahan is trying to do was the incorporation of the idea of "regressive evolution." Although this term was initially used by Lamarck (1809), it was not popularized until the beginning of the 20th century by students of cave, deep-sea, and parasitic organisms. Most of the species in those categories are characterized by the loss or reduction of a number of phenotypic characteristics such as, for example, eyes and pigmentation. Thus, these organisms became a paradigm for those who believe that evolution was in fact progressive and had a direction, a direction aimed at "improving" the organism as reflected in its structural complexity (Romero 1985).

Yet a closer look at the processes and common characteristics of these examples of regressive evolution leads us to believe that there is neither a direction in which to regress nor a special mechanism involved in the evolutionary patterns associated with them. In fact, this phenomenon can be explained by nondirectional mechanisms that take place at any level of the organic evolution.

Among the hypogean (cave) fauna, for example, we find thousands of species of troglotic (obligatory cave) organisms characterized by the lack of eyes and pigmentation. The loss of

these phenotypic features can be easily associated with a fundamental difference between their environment and that of most other animals: troglotic live in permanent darkness. Absent a selective pressure that favors the maintenance of light-related features such as eyes and pigmentation, those features are lost through time. However, this trend is not as simple as it appears. Some of these organisms show a phenotypic reduction in some features, whereas others show an enhancement of some non-visual sensory systems. Thus, these organisms seem to respond not to a particular trend, which would characterize regressive evolution, but rather to the specifics of each environmental conditions in which they have evolved (Sket 1985).

To explain the more generalized trends of blindness and depigmentation, we do not need to look for novel or exceptionally rare explanations or terms. Troglotic are a perfect example of convergent evolution, a standard evolutionary phenomenon explained by natural selection. What happens is that convergent evolution remains one of the most overlooked evolutionary phenomenon, and has yet to be subjected to a single synthesis (Conway Morris 1998).

Shanahan argues that "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 different lineages)" (p. 456), but this is precisely the problem: Convergent

evolution is an equal-opportunity mechanism that acts regardless of lineages. After all, troglotic organisms represent a vast array of species belonging to lineages ranging from arthropod and nonarthropod invertebrates to vertebrates.

Shanahan also argues that "there may 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" (p. 457). Yet thousands of examples not only from cave organisms but also from endoparasites, deep-sea animals (including organisms inhabiting deep-sea vents), underground mammals, and flightless insects and birds from islands argue otherwise. These organisms have undergone structural simplification in response to environmental constraints.

As an example of progressive evolution, Shanahan writes that "eyes have undergone progressive evolution from simple pinhole camera-type eyes to the complex eye of the hawk" (p. 458). Yet blindness or reduction of the visual apparatus can be observed not only among the organisms mentioned above but also even among cetaceans that live in the murky water of some rivers.

To assign to evolution the property *progressive* is at best confusing and at worst a vestigial, neo-Lamarckian notion of what evolution is all about. After all, the initial proponents of progressive evolution and regressive evolution have been closely associated with the neo-Lamarckian movement in both North America and continental Europe, which lasted until the modern synthesis was accepted (and lasted even longer in France). According to the *Oxford English Dictionary*, *progression* means the action of stepping or moving forward or onward. The question is, "Forward to where?" Shanahan seems to indicate that

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such movement is toward "improvement." For years we have used the term *increased fitness* in biology, a well-defined and closely argued evolutionary concept that clearly states what we mean in terms of chances for survival. We do not need vague new terms that incorporate philosophical notions lacking empirical evidence such as orthogenesis (directionality) and smacking of neo-Lamarckism.

Although classical definitions of evolution have gravitated from the Darwinian notion of "descent with modification" to the neo-Darwinian concept of "changes in gene frequency," perhaps one of the most apt descriptions of evolution was given by Dobzhansky (1970), who wrote that evolution is opportunistic, as biodiversity on Earth exemplifies. Unlike progressionism, opportunism is a well-established concept in ecology, easy to understand and to test experimentally.

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RESPONSE FROM SHANAHAN:

In my essay "Evolutionary Progress?" (*BioScience* 50: 451-459), I suggested that "the debate about evolutionary progress might have been all right once, but it has gone on too long." Evidently some biologists feel otherwise.

Dr. Romero contrasts "evolution as opportunistic" with "evolution as directional," and simply takes for granted that the first description precludes the

second. But one of the aims of my essay was to move thinking about evolutionary progress past such simplistic dichotomies by asking what *precisely* is required for evolution to be directional (or progressive, or both), and whether the satisfaction of these requirements might be consistent with the agreed-upon opportunistic character of natural selection. One way in which evolution could be both opportunistic and directional, I suggested, is if more opportunities for adaptive advance exist in one direction than in another (Maynard Smith 1970). How often this condition is satisfied is an interesting question to be answered through theoretical and empirical investigation, not by dogmatic pronouncements.

Romero complains that I claim "evolution is progressive, directional, and embodies improvement." If only life were that simple. (And I do mean *life*.) As I argued in my essay, concepts such as *progressive*, *directional*, and *improvement*, taken without careful qualification, are simply too blunt to provide any insight into the evolutionary process. He also complains that terms like *progressive* and *improvement* are vague and confusing. Indeed they are, which is why I devoted considerable space in my essay to disambiguating them. But then most genuinely interesting concepts are like that. If he really thinks that "fitness" is by contrast a well-defined concept in evolutionary biology (as distinct from being eminently useful, which is a quite different matter), I can only refer him to any of the serious discussions of this term, which clearly demonstrate otherwise (e.g., Dawkins 1999).

In his letter, Romero discourses at length on the fascinating features of cave organisms, his area of specialization, along with other organisms that have undergone structural simplification, apparently unaware that the points he makes have no bearing on my essay's argument. Of course there are innumerable cases of "regressive evolution." Every biologist since Darwin has been well aware of this fact, which is why I devoted considerable space to distinguishing the three different senses in which the evolutionary process might

have a direction: uniformly, on average, or in the increase of various maxima. The fact of regressive evolution undermines only the first of these, which, so far as I know, no biologist takes seriously anyway. (Nonetheless, cave fish are cool.)

Mysteriously, Romero interprets my essay as promulgating some sort of Lamarckian, orthogenetic vision of evolution. But the qualified conception of evolutionary progress that I discussed sympathetically is essentially the same as that defended by Simpson (1949) and more recently by Ayala (1988), neither of whom has been accused of harboring dark Lamarckian fantasies about evolution. I see no reason why my essay should cause consternation among the self-appointed custodians of Darwinian purity.

In what sense, then, is evolution "progressive"? As I made clear in my essay, a minimal condition for evolutionary progress is that there be at least some gradual directional changes in the history of life that embody improvement relative to some standard. This is an extremely modest conception of evolutionary progress, veering dangerously close to self-evident, and a far cry from some of the more grandiose proposals that have been advanced. Alas, with some topics no amount of careful explanation can preclude misunderstanding arising from adherence to deeply entrenched doctrines. I can only invite readers (and Romero) to read my essay with the intention to understand first, and to pass judgment second. Then a serious discussion can occur.

I conclude that debates over evolutionary progress have gone on long enough; but I doubt very much whether the end is in fact anywhere in sight.

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