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# CAN EVOLUTION REGRESS?

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*Abstract: An analysis of the idea of "regressive evolution" is made under semantic, historic, and descriptive viewpoints and is concluded that the term does not accurately describe the evolutionary trend toward reduction or disappearance of features in, among others, cave and deep-sea animals. Since the trend of reduction can be described and explained using the current evolutionary conceptual framework, it is proposed that we eliminate "regressive evolution" as a descriptive term for what are really only examples for convergent evolution.*

## Introduction

The term "regressive evolution" is used to describe the trend toward reduction or disappearance of features. It is frequently applied to the evolution of parasites, deep-sea animals and, especially, cave organisms lacking eyes and pigmentation. Vestigial characters in termites, flightlessness in insects and birds, and limb loss in tetrapods have also been offered as examples. The aim of this paper is to show that from semantic, historic, and descriptive standpoints, the term "regressive" does not accurately denote such evolutionary trend. I will also argue that there is no evidence for "regressive evolution" as a unique mode of evolution, and that for the kinds of changes to which it refers and the mechanisms involved, current evolutionary terminology provides an adquate conceptual framework.

## Semantics

Although many authors (e.g. Culver, 1982; Kosswig, 1965; Thines, 1969) have included detailed treatment of regressive evolution, none has concisely stated the meaning of the term. The earliest uses of this term were by Lamarck (1809) and Weissman (1889). They considered any loss in structural complexity to be "regressive" evolution, a not too helpful definition because all lineages lose (and gain) features during evolution. Other authors, such as Heuts (1953), have been even more obscure by defining "regressive evolution" as "any loss of internal stability in the organism."

The Oxford English Dictionary defines the term regressive to mean "returning, passing back, acting in a backward direction." Similar meanings are given in dictionaries of other languages where this word has been used in the same evolutionary sense. Based on this definition, the question "going back to what?" immediately arises.

The term "regressive is also problematic in an ontogenetic sense. If the point is that the adult stage reverts to earlier stages of development, then it should be remembered that some cave organisms show the same features (including eyes) in early stages of development as their "unregressed" ancestors (Cahn, 1958; Durand, 1976; Eigenmann, 1909; Thines, 1969; Wilkens, 1980).

## Historical Background

For the last two centuries, evolution has been largely perceived as something "progressive." Lamarck (1809, p. 54) considered evolution a force that "gives to animal life the power of progressively complicated organization." That view was held as a fundamental truth by the first biologists dealing with cave organisms (Agassiz, 1853). Later researchers of cave animals adopted some sort of neo-Lamarckism (Packard, 1894) but orthogenetic (directional) views of evolution rapidly became popular among biospeleologists (Lankester, 1893a,b; Jeannel, 1950). Vandel (1965) adopted an "organicistic" interpretation of orthogenetic evolution in cave animals which held that all phyletic lines pass through four evolutionary stages: rejuvenation, adaptive radiation, specialization, and "phyletic senescence." Vandel (1965) rejected any intervention of the environment during the process: blindness and depigmentation were not common to organisms because they live in caves, but because they were blind and depigmented and represented a "dying phylogenetic line," they invaded the caves (they could not survive elsewhere) (Barr, 1968).

These orthogenetic ideas were extremely popular among European biologists (except in the United Kingdom). Theilhard de Chardin (1959), for example, saw in evolution "only an event, the grand orthogenesis of everything toward a higher degree of imminent spontaneity." However, as Dobzhansky (1970, p. 391) pointed out, "attempts to define what constitutes progressive have met with only mediocre success since mere change is not necessarily progress."

## Description Problems

Clearly the structural reduction (such as blindness and depigmentation) that have been used as the descriptive components of "regressive" evolution do exist, regardless of the inaccuracy of the term employed for phenomenon. When compared with their light-adapted ancestors, deep-sea and cave organisms provide a number of cases in which an increase in the number and/or elaboration of features have been documented. In addition to the classical examples of an increase in the number and size of sensory buds in amblyopsid fishes (Poulson

and White, 1969), and in the teleost *Astyanax fasciatus mexicanus* (Schemmel, 1967), the literature of the last several years offers many new examples of increase in size or elaboration of features including hypertrophied chemosensory and tactile organs in Hawaiian lava cave arthropods (Anhearn and Howarth, 1982), new sensory organism in crustacea mysidacea (Crouau, 1978), new amino acid-derived compounds in biochemical pathways of cave sponges (D'Ambrosio et al., 1982), and hyperdeveloped buccopharyngeal membranes in cave salamanders (Serra and Stefani, 1981).

Although there are also cases of troglobites in which neither sensory compensations nor morphological enlargements have been described (Culver, 1982) there is no question that the evolution of cave organisms involves much more than simply a few structural reductions. Emerson (1961), for instance, recognized "associated progressive and regressive evolution" and Kosswig (1973) mentions instances of "constructive" evolution during "regressive" evolution.

## The Mechanisms

Besides semantic, historic, and descriptive problems, is there a unique mechanism responsible for "regressive" evolution? Experimental studies indicate that well-known mechanisms are sufficient to explain the reduction in features. Selection, pleiotropy, differential migration, "noise" suppression, and ontogenetic buffer mechanisms have been implicated (see Barr, 1968; Culver, 1982; Katz et al., 1981; Lande, 1978; and Regal, 1977). In consequence, no evidence has been provided supporting the assertion that "regressive" evolution is different from other kinds of evolution.

## Is a New Term Necessary?

The question is if the term "regressive" is inaccurate from many viewpoints, how should we refer to this common trend among many organisms? Previous attempts to solve this problem have not been very successful. The term "degenerative" evolution (Eigenmann, 1909) poses not only the same conceptual problems as "regressive" evolution but also adds a pathological angle. The terms "rudimentation" (Dobzhansky, 1970) and "structural reduction" (Brace, 1963) seem the least problematic terms; however, they do not apply to changes in behavior and physiology, since they refer only to specific structures and do not describe the trend as a whole. The terms "streamlining" evolution (Regal, 1977) and "channel" evolution (Katz et al., 1981) present similar descriptive problems.

Gould and Vrba (1982) have pointed out that in biology "unnamed ideas generally remain unconsidered." However, the trend observed in cave animals has been recognized since the discovery of the first cave organisms regardless of the nomenclature used for it. On the other hand, and for practical purposes, it is convenient to have a term with which one can concisely express a set of ideas or observations. The following attributes characterize obligate cavernicoles (troglobites) and are seen in many lineages: the animals live in a subterranean environment and exhibit at least two common features that are universal (blindness and depigmentation) and others that seem to be widespread at least for organisms at upper trophic levels: enlargement, multiplication and/or appearance of new sensory structures, larger size, and low metabolic rate.

In general, when unrelated species occupying similar environments share a number of characteristics, the term "convergent evolution" is applied. Cave animals provide, in fact, one of the best examples of convergent evolution. Why then is this term not frequently employed by researchers of these organisms? Several reasons can be offered: first speleology has had its major development in continental Europe (especially in France) where Darwinian ideas were not very popular (Vuilleumier, 1984). Second, in continental Europe the defense of evolution as a fact was carried out by Catholic priests such as Theihard de Chardin who envisioned evolution as an orthogenetic perfectionist process in which selection and environment play no role at all. Only in the last 20 years has this orthogenetic and/or neo-Lamarckian tradition been challenged by a few neo-Darwinists and proponents of the neutral mutation hypothesis, and these workers object to the term convergent evolution because, many say, it is the product of directional selection which has yet to be demonstrated to occur during the evolution of cave organisms (Barr, 1968; Culver, 1982; Wilken et al., 1979).

Let us banish "regressive evolution" from our vocabulary. If we use the term convergent evolution in its strict sense (independent acquisition of similar features by unrelated organisms that live in similar environments), then it aptly describes the evolution of cave-dwelling animals. In any event, we should not forget that this convergence is precisely what we are trying to explain in the first place.

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*Postscript:* After this manuscript had been submitted for publication, a paper was published in which conclusions similar to the ones presented here were reached. [Bannister, K.E. 1984. A subterranean population of *Garra barreimae* (Teleostei: Cyprinidae) from Oman, with comments on the concept of regressive evolution. *J. Nat. Hist.* **18**:927-938].

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