Cave Controversy

To the Editors:

Nine biospeleologists from Brazil, Slovenia, the United Kingdom and the United States find that Aldemaro Romero's "The Evolution of Cave Life" (March–April 2011) misrepresents our current and past views. Thomas C. Barr, Kenneth Christiansen, Annette Summers Engel, John Holsinger, Matthew Niemiller, Graham Proudlove, Boris Sket, Eleonora Trajano and I work in different aspects of biospeleology on different organisms and have written hundreds of peer-reviewed papers over the past 50 years. On the basis of our wide experience and research, we find that Romero gives, at worst, a biased view and at best a minority view of important aspects of biospeleology. We fear that the naive reader will be misled by his erroneous subtitle, "New concepts are challenging conventional ideas about life underground." We find:

- Errors of terminology (e.g., troglobitic vs. troglomorphic) and biology (e.g., one-third of hypogean fish are fully eyed and pigmented).
- Misrepresentations of the data and conclusions of our published studies. Not one of us argues that troglomorphic characters necessarily develop in parallel. Nor do we argue that caves are so constant that no ecological fluctuations take place.
- Incorrect characterization of our views as unitary and neo-Lamarckian. We argue concepts all the time, and we are all strong Darwinists.
- "Straw-man" arguments, especially about pre-adaptation and archetypes. None of us has written that all troglobites had ancestors that were preadapted, and not one of us believes in an archetypical hypogean species.
- Exclusive emphasis on his single hypothesis of the centrality of phenotypic plasticity for the colonization of caves. We explore all of the multiple hypotheses for colonization or isolation in caves.
- Exclusive emphasis on only one study system, that of the cave and surface Mexican *Astyanax* fish, for which only some populations support some of his views.

Romero's article is not as strident as his 2009 book, *Cave Biology: Life in Darkness*. But our general areas of concern and disagreement with his article are the same as those several of us presented in reviews of his book. These include my review in the spring 2011 issue of *Bioscience* and Engel's review in the October 2010 issue of *Integrative and Comparative Biology*.

Thomas Poulson
Jupiter, FL

To the Editors:

I felt dissonance reading Aldemaro Romero's cave article. Although a focus on his own research was understandable, his general approach and lack of reference to other pertinent work implied that biospeleology was in disarray, which it is not.

For example, Romero used definitions for troglobite and troglophile that were based on troglomorphic characteristics, troglobites being very troglomorphic and troglophiles being less so. More customary definitions are based on how strongly troglobites and troglophiles are confined to caves—troglobites being obligate cave dwellers, but troglophiles being able to live both in and out of caves. Troglophiles often show no apparent troglomorphisms

Illustration Credits

Computing Science
Pages 192–194 Brian Hayes

Marginalia
Page 201 Tom Dunne

Ethics
Pages 205, 206 Tom Dunne

Global Energy: The Latest Infatuations
Figures 2–4, 7 Tom Dunne

Marking Loons, Making Progress
Figures 3, 5, 7, 9–11 Tom Dunne

Pliocene Climate Lessons
Figures 2, 4–8 Barbara Aulicino

Porphyrins: One Ring In the Colors of Life
Figures 2, 5 *(right)* Barbara Aulicino

due to ongoing genetic exchange with epigean relatives. Troglobites, which lack such exchange, tend to show considerable troglomorphism, and those that have been isolated in caves the longest show the most. Throughout his article, Romero neglected to emphasize the importance of isolation to the development of troglomorphisms, and the definitions he chose for troglobite and troglophile also ignored the concept of isolation.

As another example, Romero discounted the phenomenon of entrapment as a likely step toward living in a cave, but failed to explain the well-grounded example of how Ice Age climate change could do just that. For example, if the surface environment became too dry for a particular troglophile, that troglophile would be trapped in its damp cave, epigean relatives would depart or die due to the dry conditions, and gene flow from the surface would stop. The stage would then be set for evolution toward greater cave adaptation. This loss of gene flow from surface relatives answers a question Romero posed about why some hypogean species undergo major phenotypic changes while others remain similar to their epigean ancestors.

Although this article presented many interesting observations about cave life, it failed to integrate them into our broader understanding of how cave life evolved, particularly with regard to the role played by isolation, the length of that isolation and our understanding gained through comparative biogeography.

Norman W. Youngsteadt
Springfield, MO

To the Editor:

Aldemaro Romero's excellent and informative article on cave animals not only makes good points about the adaptive genetics of cave life but also illustrates how organisms of choice can affect conclusions. This speleobiologist, who focuses on troglobiotic terrestrial arthropods in temperate climates, sees some matters differently from one who studies aquatic vertebrates in mostly tropical environments. As an example, Romero does not mention the climatic relict hypothesis of cave invasion in answering the question of how animals get into caves to begin with. In this idea, the ancestors of troglobionts are not cave invaders by choice (as Romero's fish might be) but are marooned in caves when the climate outside changes drastically and surface populations become locally extinct. Similarly, since most cave arthropods are members of taxa which inhabit cave-like places such as the soil and leaf litter, preadaptation to those habitats very likely plays a role in their success in caves. In order to fully understand the evolution of cave animals it is necessary to examine a wide spectrum of taxa.

William Shear
Hampden-Sydney College

Dr. Romero responds:

The letter from Thomas Poulson et al. makes a number of claims that are not substantiated by reading my article. The researchers claim that I misrepresent their views even though they are not even mentioned in the article. They also claim that I emphasize a single hypothesis or study system when describing certain phenomena of cave life. That was precisely the point of the article: to show that there are data challenging the orthodoxy carried forward by some people for some time. To examine the full range of hypotheses and ideas, readers may wish to look at my 2009 book.

From reading their letter it is clear that the main contention of these authors is that I do not adhere to the right orthodoxy. As I analyzed in great detail in chapter 1 of my book, supported by extensive documentation, biospeleology is a field that has been plagued with intellectual inertia over time. If the history of science teaches us anything, it is that change is the only constant and that change must be generated by data, such as those I present in my book and article.

In response to Norman Youngsteadt: My book cites the conventional hypotheses about cave colonization. On the issue of definitions I have purposely moved away from the typological approach to the classification of cave organisms because, like many modern biologists, I do not believe that species are members of a periodic table like the elements of chemistry. Data cited in my book strongly suggest that there is simply too much flux in their ecological and morphological characteristics to believe that all cave populations can be boxed into predetermined types. Regarding isolation, Youngsteadt's reference to the Ice Age is not an example but a hypothesis that has not been corroborated by experimental data. The hypothesis is disqualified as a valid generalization to explain cave colonization if we consider that the vast majority of cave biodiversity is found in the tropics and not in temperate environments (where most cave biologists have traditionally done their studies), and that a large portion of cave populations that display characteristics typically associated with life in darkness date back well before any particular Ice Age.

Shear makes a good point that terrestrial and aquatic organisms will have different restrictions when it comes to dispersal in caves, something I mention in my book. When I refer there to the climatic relict hypothesis, I note that so far the idea lacks empirical evidence; further, its assumptions cannot be generalized to all cave organisms, the vast majority of which are found in the tropics. As I also show in my book, available data do not support the idea of preadaptation as a general explanation for successful colonization of caves. Other characteristics of an organism such as being ecological generalists, probably combined with genetic heterozygocity, likely play an important role. That is also noted in my book, which includes a survey of all taxa represented in caves, from bacteria to mammals. As Theodosius Dobzhansky pointed out, evolution is opportunistic. Cave biotas are a good example of that.

How to Write to *American Scientist*

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Errata

Owing to a typographical error in "Arches and Domes" (March–April), the photo caption for the Hagia Sophia indicates that Christians and Muslims fought over the structure in the 5th century rather than the 15th.

In "The Evolution of Cave Life" (March–April) Figure 8 shows a skeleton on a cave floor labeled a swiftlet. It is actually a bat.