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The Evolution of Cave Life

New concepts are challenging conventional ideas about life underground

Aldemaro Romero

In a famous anecdote from the history of biology, a student of French naturalist Georges Cuvier is said to have shown up in Cuvier's bedroom dressed like a devil, horns and cloven hooves included, saying "Cuvier, Cuvier, I am going to eat you!" Cuvier looked at the apparition and retorted, "Horns, hooves, a tail: herbivore. You cannot eat me."

This story epitomizes how strongly we correlate forms of life and lifestyles. Animals with large eyes are assumed to be nocturnal, plants with large leaves are supposed to be from humid tropical environments, and so on. It is easy, then, to imagine that all cave creatures must be blind and depigmented; after all, what need does an animal have for eyes and pigmentation while living in perpetual darkness?

Research in the past few decades strongly indicates that affairs underground are not that simple, that in fact the ecology of the cave environment is extremely diverse and that evolutionary processes governing adaptation to that environment can be quite surprising even when explained in modern Darwinian terms.

Caves come in all shapes and forms, from caverns to lava tubes to ice caves. Some subterranean environments are never entered by humans because they lack an opening to the surface, as is the case for some underground lakes

and rivers known as phreatic environments (from the Greek *phrear*, cistern or well). The most common caves are karstic or limestone. Because limestone is a highly soluble rock (at least 50 percent calcium carbonate), karst is easily modified by acidic rainwater. This type of landscape covers about 15 percent of the Earth's dry surface. One hundred thousand caves have been described in Europe and about 50,000 in the United States.

From bacteria to mammals, tens of thousands of living species have been described for cave environments and many more are yet to be discovered, especially as we have finally gotten serious in recent years about exploring the rich and relatively overlooked biota of tropical caves.

Generally biospeleologists divide the world in two: the epigeal (epi-, upon, -geal, earth) and the hypogeal (hypo-, under) environments. The former refers to the world outside caves that is exposed to light directly or indirectly on a regular basis; the latter represents any part of the biosphere that is found underground. The hypogeal environment includes soil or interstitial, phreatic or artesian, and cave. The term *cave* is reserved for those underground habitats that can be directly explored by humans.

The degree of exposure to light is one of the characterizing features of the hypogeal world. A fascinating case in biospeleology is the existence of caves with overhead openings that allow the passage of light. In those areas of caves where light interrupts what is otherwise total darkness, we can find eyed, pigmented organisms like those normally found outside caves. Sometimes those organisms belong to typical epigeal species; sometimes they are eyed, pigmented forms of hypogeal ones.

An example of the morphological differentiation among individuals of the same species is the case of the characid fish *Astyanax fasciatus*, a tetra that inhabits the Sótano del Caballo Moro cave in Mexico. At some unknown time in the past, part of the ceiling of that cave collapsed, allowing light to illuminate part of one of its underground lakes. Blind, depigmented individuals are found preferentially in the dark side, while eyed, pigmented fish are found in the illuminated side. Interestingly, genetic analysis revealed that the cave-dwelling eyed fish is closer to the blind fish than to the surface population. This finding suggests that the cave eyed fish were originally members of the cave population and reacquired eyes and pigmentation following the collapse of the cave ceiling and exposure to the light.

Hypogeal organisms are grouped based on their morphology and behavior. The most popular system of classification defines *troglobitic organisms*, those always showing *troglophormisms*, meaning cave-associated characteristics (*characters* in the language of taxonomics) such as total blindness and depigmentation; *troglophilic organisms*, those showing some degree of reduction in those characters; *trogloxenes*, organisms not showing such reductions but still spending significant portions of their lives in caves (for example, some bat species), and *accidentals*, those apparently present in caves by happenstance and not because they normally live there. Notice that *accidental* is an ad hoc definition: In theory, when an individual of a species that later may become a permanent inhabitant of caves first enters a cave, it could also be called an accidental. Furthermore, there are many species of animals that spend their entire life cycles in the hypogeal environment yet do not show any ap-

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Figure 1. The blind cave tetra, *Astyanax fasciatus*, shows a classic morphological emblem of life in permanent darkness, eyelessness. Darwin himself tried to explain what he called *rudimentation*, or loss of morphological apparatus through evolution underground. Recent field work in biospeleology and a deeper understanding of the genetics of development are now informing many aspects of modern biology.

parent morphological feature associated with their underground habitat.

In the quest for an archetypal definition of cave organisms, biospeleologists have been obsessed with troglomorphisms such as blindness and depigmentation. Yet we must ask, is there truly a hypogean archetype that fits most if not all hypogean organisms? And if it is possible to define such an archetype, does it have significant evolutionary meaning?

In most of the biospeleological literature, the same set of troglomorphic characters appears consistently as distinguishing features of cave organisms (Figure 3).

The first challenge to accepting a hypogean archetype is that phenotypic characters may be enlarged or enhanced as well as diminished among these organisms. The rules are not consistent. Most changes in morphological characters are associated with the absence of light. Reduction of the visual organs, whether eyes or ocelli (primitive eyelike organs found in some invertebrates),

is considered a rule for troglomorphic organisms; yet there are many exceptions. One is the cyprinid fish *Sinocyclocheilus macrophthalmus*. Other species of this same genus found in caves in China are blind or have reduced eyes and are depigmented, but this particular cave species, although it is depigmented, has eyes larger than those of any other species in the genus, including the epigean species. Having large eyes is an unusual adaptation for fish, but it is common among nocturnal vertebrates.

The enlargement of the size of sensory organs is not necessarily the rule for other troglomorphic organisms: The phreatic Texas blind catfish *Trogloplanis pattersoni* has rather minute barbels (whiskerlike sensory organs near the mouth), whereas most hypogean catfishes tend to have larger barbels than those of their epigean ancestors. Similarly, metabolic rate is commonly reduced in troglomorphs, yet the Mexican cave tetra *A. fasciatus* has nearly twice the basal metabolic rate of its epigean form.

Degrees of troglomorphisms such as blindness and depigmentation can be highly variable among different species. In results obtained by Kelly Paulson and myself, from a carefully sorted sample of the 86 species of troglomorphic fishes known at the time, only seven had the same level of troglomorphism for each one of those characters (Figure 4). Furthermore, when all the characters were combined in a phenotypic landscape, the results showed a very diverse mixture of character development, subtracting support from the hypothesis that troglomorphic characters necessarily develop in parallel (Figure 5). To explain such a mosaic of morphologies, it is plain that we must take into account both the evolutionary history of the species involved and the peculiar characteristics of the environment in which they live.

To make things even more complicated, a large number of hypogean species do not show any kind of troglomorphisms. For example, as of August 2008, 299 species of fishes had been

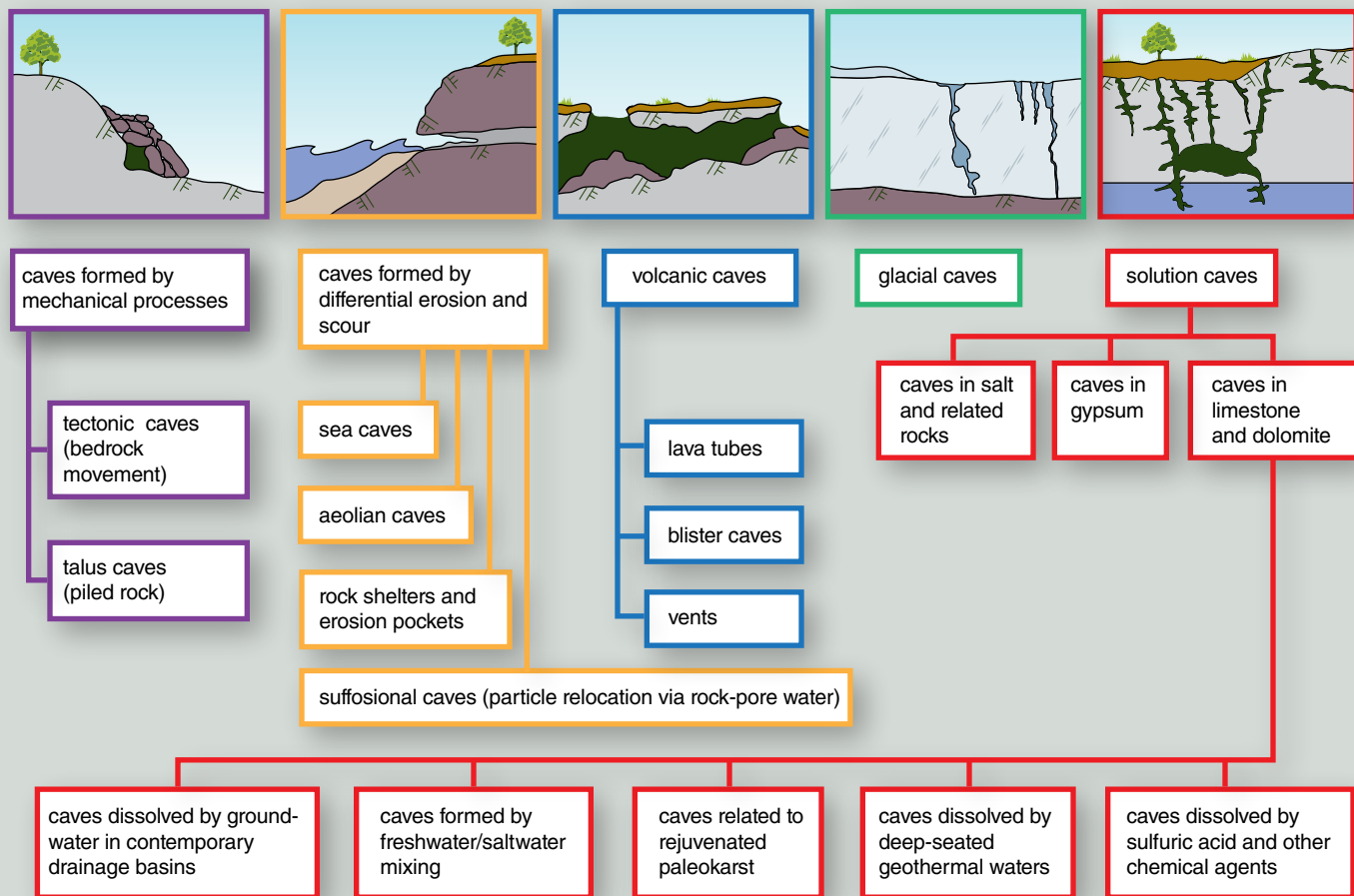


Figure 2. Caves are formed where the Earth is scooped, torn, worn, heaped, dissolved or blasted by volcanic flows. Organisms that find their way in may leave behind stressors such as natural predators, but in many cases they take on severe ecological challenges—not just total darkness, but also low total energy in the ecosystem, spare biodiversity and peculiar hydrology. Yet most caves host a thriving biota.

	morphological	physiological	behavioral
reduced or lost	eyes, ocelli (primitive invertebrate eyes) visual brain centers pigmentation pineal organ body size cuticles (terrestrial arthropods) scales (fishes) swim bladder (fishes)	metabolism circadian rhythm fecundity egg volume	photoreponses aggregation response to alarm substances aggression
enlarged/ increased	chemo- and mechanosensors appendages body size	life span lipid storage	

Figure 3. Troglomorphisms are characters associated with cave organisms. They may include adaptive changes in organ structure and function, metabolism, life history and behavior. (Sensu Christiansen, K. A. 1962. In Camacho, A. I., ed. *The Natural History of Biospeleology*. Madrid: Museo Nacional de Ciencias Naturales, pp. 453–78.)

reported living in the hypogean environment. Of those species, 184 have been described as having some kind of troglomorphisms. In other words, about one-third of hypogean fish species are fully eyed and pigmented.

Another confounding variable is that not all troglomorphisms can be explained as a direct consequence of the absence of light. An example is reduction or loss of scales among cave fishes. On the other hand, a functional explanation for the diminishment of the gas (swim) bladder among hypogean fish is more readily apparent. Hypogean waters tend to be very shallow, so the adaptive value of this organ disappears.

The emerging picture from the information summarized above is one of complexity and even contradiction. It certainly does not support blanket generalizations about the phenotypes of hypogean fauna. In other words, there are no archetypal hypogean organisms. We simply cannot make strong empirical generalizations about

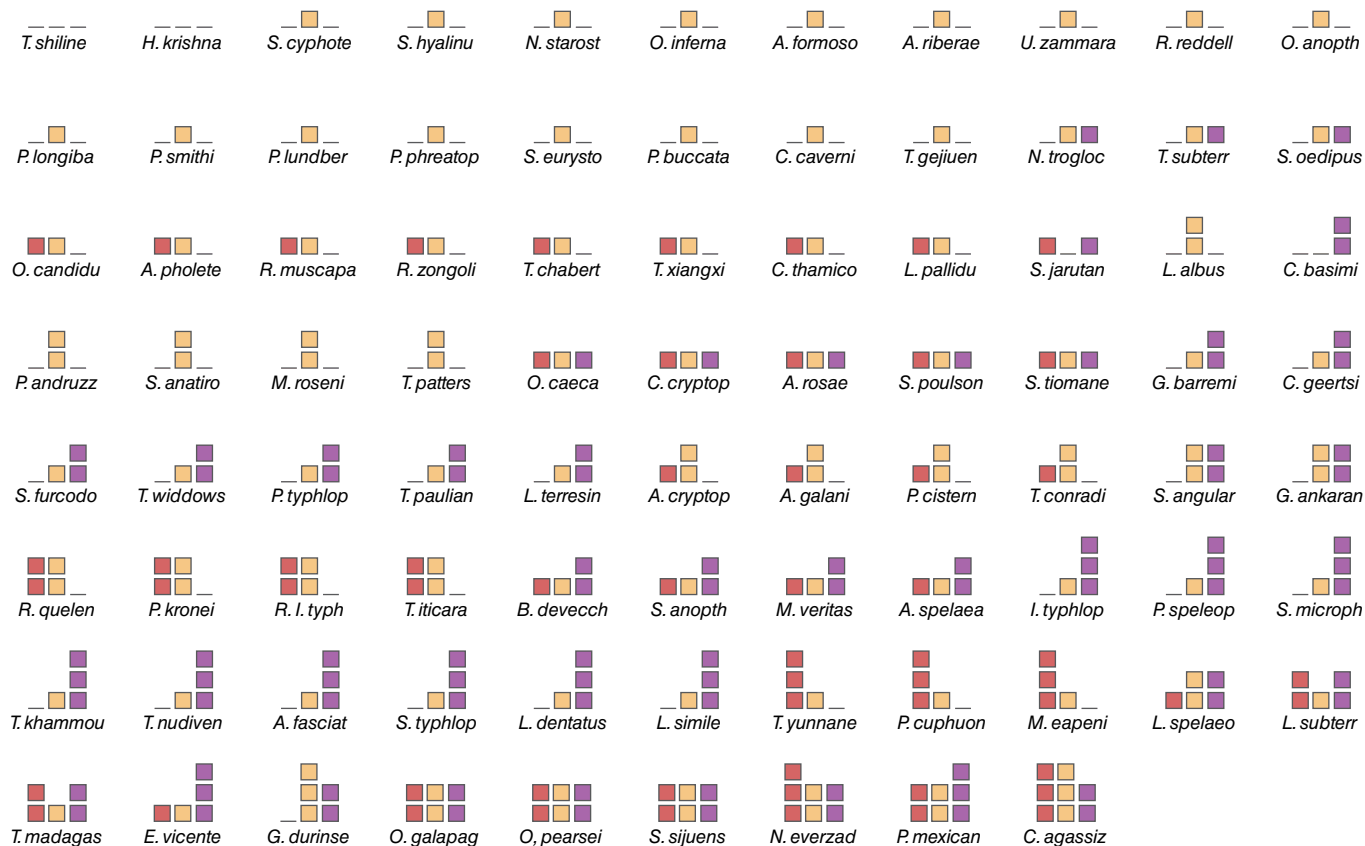
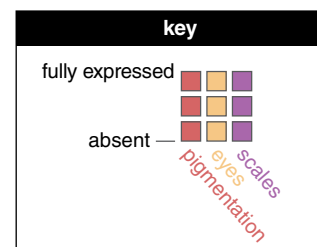


Figure 4. This chart specifies the character state for eye condition, pigmentation and scale development for 86 species of troglomorphic fish, all that were known at the time the data were assembled. A brief scan of the developmental trends reveals that the adaptive pressures are quite inconsistent, indicating that generalizations about the evolution of troglomorphisms are unreliable. Where comparative selective pressure was apparently weak and strong on two specific characters in one species, it can be found to be strong and weak, respectively, in another species. (Species names are abbreviated. For complete names, see Romero, A., and K. M. Paulson. 2001. It's a wonderful hypogean life: A guide to the troglomorphic fishes of the world. *Environmental Biology of Fishes* 62:13–41.)



how each character trait affects individual fitness. Natural selection does not allow such easy predictions.

Getting There

Colonization of hypogean environments is a biological phenomenon riddled with controversy and speculation, largely because the process is difficult to observe in natural conditions. Further, most biospeleologists, whose field experience is largely confined to temperate, low-energy caves, have always assumed that there are no really good reasons why an organism would occupy a nutrient-poor habitat. Therefore, many have espoused the idea that colonization of the hypogean environment occurs only by accident or by some unusual circumstance. Yet field observations contradict such notions. Part of the argument for happenstance colonization is that once organisms get into hypogean environments,

they only stay if they are trapped. But whether the cave colonizers reach the hypogean habitat by flying like insects, scuttling like arthropods or creeping like salamanders, there is apparently little that prevents them from returning by the same route to their original habitat. The accidental-entrapment hypothesis is but a weak generalization for the process of cave colonization.

Are there field observations that support some particular explanatory mechanism for the colonization of the hypogean environment? I carried out studies at a pond in Costa Rica that receives water from a phreatic source, a spring whose outlet was unviewable below a low ceiling of rock. An assemblage of about 120 epigeal Mexican tetras, *A. fasciatus*, living in that pond were morphologically identical to other epigeal tetras, with full eyes and pigmentation. However, I found that unlike the typical epigeal population, the fish in the

pool did not form schools. Schooling behavior is often lost in cave fish populations. Furthermore, when I dropped floating food onto the surface of the water, the fish, almost without exception, pushed the food to the subterranean habitat before consuming it. A number of field observations and experimental manipulations of fish environments strongly suggest that fish both pushed the food into the subterranean cavity and also disappeared into that cavity at night to escape fishing bats of the species *Noctilio leporinus*. These observations suggested not only that *A. fasciatus* was using the underground pool as a shelter from bat predation, but also that the tetras may have been in the process of colonizing the underground waters as a response to selective pressures, not by accidental exposure.

The idea of active colonization has also been proposed for ice caves in temperate regions. (Ice caves are

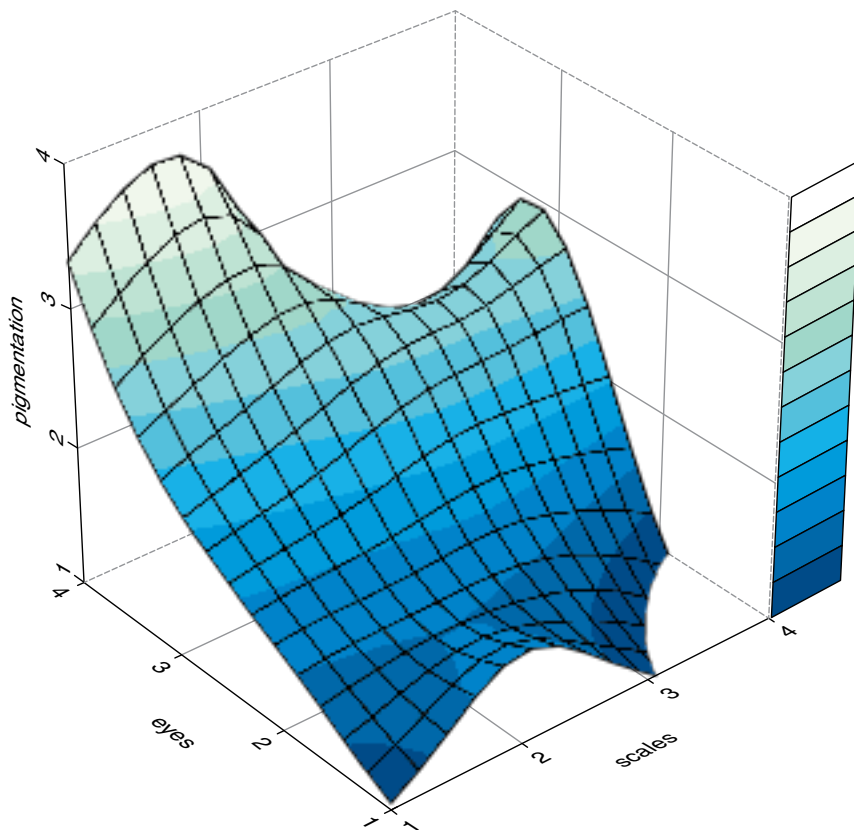


Figure 5. Biologists once supposed that the driving forces for development of commonly seen troglomorphisms were related in some way and that these changes occurred in parallel. The irregularity of this landscape representation of the character state for known troglomorphic fish species, based on the data in Figure 4, illustrates plainly that parallel development is not generally the case.

characterized by the presence of some amount of ice year round.) Plethodontid salamanders in the Cumberland Plateau of northwestern Georgia use both cave and epigean habitats, moving into caves to avoid hot, dry conditions in the epigean environment.

It is worth mentioning that some troglomorphic populations may be ecologically replaced by epigean ones, sometimes quite rapidly, and even if the epigean form is the reputed ancestor of the hypogean population in question. That is the case of the hypogean population of the catfish *Rhamdia quelen* from a cave in Trinidad. This fish population was originally described in 1926, and on the basis of its reduced eyes and pigmentation was designated a new troglomorphic genus and species, *Caecorhamdia urichi*. Beginning in the 1950s, a number of specimens collected in the cave displayed variability in eye size and pigmentation. Later studies indicated that this cave population was, taxonomically speaking, part of the widely distributed epigean catfish

Rhamdia quelen, eyed, pigmented and living on the surface. In field studies conducted in 2000 and 2001, my collaborators and I examined all available specimens of the cave population and those that had been deposited in museums. Our results suggested that the troglomorphic population had been completely replaced by the epigean one of the same species in as little as 50 years. Most likely the reason for this replacement was the reinvasion of epigean individuals of *R. quelen* prompted by changes in precipitation regimes. Epigean individuals, because of their larger size, more aggressive behavior and generalist feeding nature, were well suited to outcompete troglomorphic individuals.

Another question frequently asked concerns cave species that are found in several caves, connected or not. Are those populations the product of a single colonization event followed by hypogean dispersion, or are they the product of multiple colonization events? Molecular genetic studies

among cave crustaceans, insects and fish strongly suggest that caves are subject to multiple invasions by the same epigean species.

Preadaptation

Are some species more likely to be successful hypogean colonizers than others? And more importantly, why do some hypogean species undergo major phenotypic changes while others remain similar to their epigean ancestors?

An idea with considerable currency in biospeleological discourse is the concept of preadaptation. The notion is that many organisms possess features that allow them to easily adapt to a particular environment or mode of life: thus, nocturnal animals should be “preadapted” to the dark cave environment. But is there any compelling evidence that an organism has to be preadapted to successfully colonize a hypogean environment?

My collaborators and I tested the preadaptation hypothesis among troglomorphic fishes. In our survey of the literature, we found that three features were generally invoked as “preadaptations” for the hypogean environment: hyperdeveloped sensory organs, low metabolism and nocturnal habits. One, two or all three might be implicated. We then grouped the 86 troglomorphic species of fishes then known into their 18 respective families and looked for any of the above “preadaptive” characters among those families. Of the 18 fish families with troglomorphic representatives, only 10 had any of the “preadaptive” features. We concluded that alleged preadaptations to the hypogean environment are neither necessary nor sufficient for a species to successfully colonize a hypogean habitat.

Some species even contain built-in arguments against the notion of “preadaptation.” The Mexican blind cave tetra is one the most studied cave organisms. This species can be found as both an epigean (eyed and pigmented) and hypogean form (usually, but not always, blind and depigmented). The epigean form has a broad distribution in the freshwaters of the New World from Texas to Argentina. Although cave populations of the eyed form have been reported elsewhere, the only region in which they have developed into blind, depigmented individuals is in East Central Mexico, where more than 30 caves supporting subterranean populations of this fish can be found.

However, the cave populations of this area do not all display the same degree of morphological divergence from the surface forms. Some are completely blind and depigmented whereas others are only partially so. Three caves contain only individuals with full eyes and pigmentation. Eleven of these populations include blind and eyed forms, as well as phenotypically intermediate forms. At least one of them contains both eyed and blind forms with no intermediate forms.

Besides blindness and depigmentation, the troglomorphic and surface morphs of this fish differ in many other characteristics. For example, the troglomorphic populations have a larger number of taste buds, never school, are active all the time and are not aggressive. The blind form produces an alarm substance like the surface morph but does not respond to it. Differences in the level of phototactic responses among different populations have also been reported, indicating that even blind cave forms can respond to light; the level of response differs depending on the specific population.

The surface and troglomorphic forms of *A. fasciatus* interbreed in both natural and laboratory conditions, producing fertile hybrids with a phenotypically intermediate form in the first (F1) generation. In the F2 generation (after self-cross), individuals range

from an almost completely blind and depigmented form to an almost fully eyed and pigmented one. Other genetic studies also support the contention that the cave and epigean forms are the same species.

This biological picture is complicated not only in space but also in time. When the troglomorphic form of *A. fasciatus* was originally described in 1936, the entire population in that locality consisted of a very uniform morph of blind and depigmented fishes. I analyzed the gross morphology of individuals that had been collected between 1936 and 1942 as well as those I collected in 1982. I found that the La Cueva Chica population had evolved in 43 years or less into a morphologically intermediate population composed of individuals that were neither totally blind and depigmented nor fully eyed and pigmented. I concluded that this new morph was the result of introgressive hybridization—transfer of genes from one population to another via repeated crosses. The transfer probably started in 1940 with the invasion of the cave environment by epigean individuals.

With all this information at hand, no one has ever formulated a convincing description of what could have been the “preadaptive” features of *A. fasciatus*’s comparably well-studied epigean ancestor. Further, if the epigean *A. fasciatus* was indeed preadapted, why has

it undergone such massive morphological, physiological and behavioral changes to become a troglomorph?

Gaining by Losing

Now it is time to address the most intriguing issue in biospeleology: Why are some phenotypic characters lost as cave organisms evolve?

One biological phenomenon that is rarely mentioned in the biospeleological literature and that, I believe, plays a major role in both the diversity of morphs and the evolution of cave fauna in general, is phenotypic plasticity. A number of casual observations carried out by researchers on different cave fish species have suggested that cave animals and their epigean ancestors can display responses to the presence or absence of light during the development of their pigmentation and their visual apparatus.

My collaborators and I were able to confirm these initial observations by controlling the light conditions for 24-hour-old larvae of *A. fasciatus* from three different populations: epigean (eyed, pigmented), troglomorphic (blind, depigmented) and their hybrids. For a period of 30 days, some of the larvae were exposed to light 24 hours per day, others were confined to total darkness. The results showed that the eyes of the epigean larvae were much less developed when the fish were raised under conditions of total darkness than when raised under constant light. However, the most spectacular results were obtained with the cave population: Although those larvae that were raised under conditions of total darkness did not show any noticeable eye tissue, as expected, those raised under constant light conditions did.

This result strongly suggests that many troglomorphic animals evolved from epigean species by means of phenotypic plasticity. That conclusion is consistent with the fact that lack of light can trigger heterochrony, meaning changes in the timing of development of features. Examples of phenotypic plasticity can be seen in paedomorphs (animals that do not reach morphological maturity, instead reproducing as juveniles) and neotenes (animals with slowed growth). Many cave organisms are either paedomorphic or neotenic. Most troglobitic salamanders are paedomorphic, and half of all known paedomorphic salamanders are troglomorphic. Neoteny among



Figure 6. The organs of this two-pronged bristletail are clearly visible through its unpigmented cuticle. There are about 100 species of hypogean dipturans like this one, all of them blind and depigmented. All 100 species are remarkably similar, despite belonging to two different families. These similarities represent a compelling example of convergent evolution in caves. Photo by Danté Fenolio.

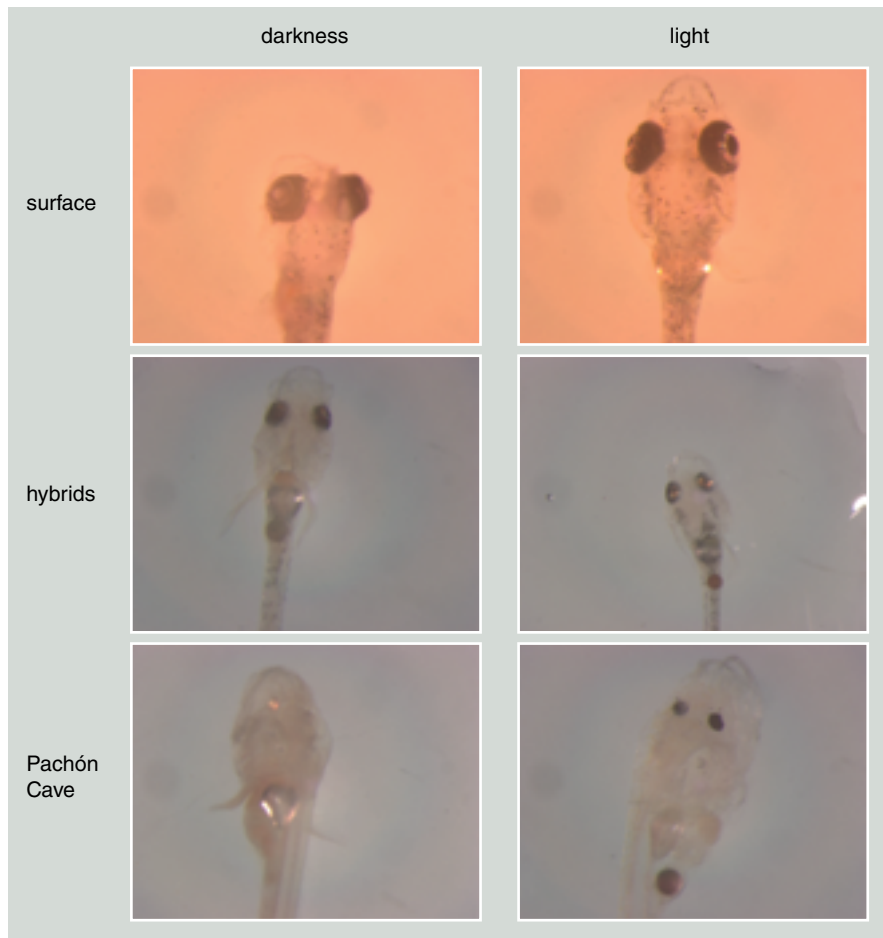


Figure 7. Phenotypic plasticity is plainly visible in the development of eye tissue and pigmentation among different populations of the cave tetra *A. fasciatus* that underwent development under different light regimes—30 days of constant light or constant darkness from the time they were hatched. The eyes of the surface species (top) are much less developed when raised in darkness; in the normally eyeless cave species (bottom), development of eye tissue is strikingly evident in the specimen raised in constant light. (Photographs courtesy of the author.)



hypogean animals, particularly fish, is well documented. Individuals living in the hypogean environment gain an advantage by becoming paedomorphic because they can reproduce earlier in their life cycle. The disadvantage that immature individuals are less able to defend themselves is obviated because cave organisms commonly do not have natural predators.

These examples also reinforce the idea that troglomorphisms are the result of natural selection and not just undirected decay of a phenotype. We know that the reaction norm—the direction and degree of a phenotypic change in response to environmental factors—is genetically variable and subject to natural selection. Therefore, natural selection may favor those individuals with a higher capacity to express specific traits under appropriate conditions. Thus phenotypic plasticity often provides a reproductive advantage over a genetically fixed phenotype because environmentally induced phenotypes have a higher probability of conforming to prevailing environmental conditions than genetically fixed ones.

I believe that natural selection favors paedomorphs and neotenes by fixing paedomorphic and neotenic alleles in the cave population. Given that most cave populations are small and subject to very similar selective pressures within the same cave, this evolutionary process can take a relatively short period of time.

This explanation is further supported by the convergent nature of troglomorphic characters. Convergent evolutionary patterns are strong evidence of adaptation via natural selection. Isolation would later lead toward speciation through genetic differentiation from the epigean ancestor. Many troglomorphic organisms are believed to have recently invaded the hypogean environment because their epigean ancestry is easily recognizable, and the cave and surface populations can even interbreed and produce fertile hybrids.

Figure 8. A swiftlet that has fallen to the floor in the Deer Cave, Sarawak, Borneo, is rapidly reduced to a skeleton by cockroaches and beetles. Caves were long presumed to be uniformly low-energy environments hosting sparse ecosystems. As biospeleology gathers momentum and more caves are explored, especially in tropical regions, a different picture of much richer biodiversity is emerging.

Indeed, we can see the same types of selection-induced changes among deep-sea fishes and fishes in murky rivers where reduction or loss of eyes and pigmentation has occurred.

How can we explain, then, why the evolution of troglomorphic characters does not necessarily occur in parallel, but instead produces the uneven array of phenotypes seen in Figure 4? First, because they are controlled by sets of genes independent from one another. Second, the degree of development of some of these characters (for example, barbels in fish) is conditioned by their phylogenetic history. Lastly, the selective pressures on each one of those characters may differ from cave to cave.

What is there to say about all the nontroglomorphic species living in the hypogean environment? We know that there is abundant genetic variation for plasticity within natural populations, which in turn is subject to selection. Also, genetic variation for phenotypic plasticity is widespread, and the same population can harbor genetic variation for the plasticity of one trait while being invariant for the plasticity of another trait related to the same environmental variable. Again, this may explain the complexity observed in phenotypic responses among hypogean organisms. Some may display a high degree of blindness but very little depigmentation because the genes controlling one of the features are highly plastic while those controlling the other are not.

The ability of individuals of some troglomorphic species to regain some eye tissue and pigmentation, as reported here, may be the result of each population's retention of a substantial capability to alter its phenotype even if it represents an ecotype—a population that is genetically specialized to a particular environmental condition. This concept fits perfectly with our knowledge of population genetics for *A. fasciatus*, in which we find drastically different phenotypes (epigean and troglomorphic) yet very little genetic differentiation. The troglomorphic type could easily be characterized as an ecotype. A phenotypically plastic genotype could yield what looks like an ecotype under extreme environmental conditions. Substantial convergence in the reaction norm of different populations can occur within certain ranges of environments.

Plasticity can (and should) be maintained in fluctuating environments, especially when fluctuations in the envi-

ronment are predictable to some extent. Another longstanding generalization about the cave environment is the belief that caves are so constant that no ecological fluctuations take place in them. However, this view has been under challenge for some time. Flooding, for example, is a relatively common periodic event in caves and represents a striking fluctuation in ecological conditions.

It is not surprising that cave organisms for which phenotypic plasticity has been demonstrated are all aquatic: sponges, crayfish, fishes and salamanders. Fluctuating environmental conditions are common in tropical caves where there are constant (but predictable) variations in water level due to drastic seasonal changes in rainfall, which helps to explain why there are more troglomorphic species/populations in lower latitudes than in temperate regions.

Caves represent unique natural laboratories. They have served as a spring of biological ideas in the past, and they still provide us with an excellent venue for confirming and expanding our view of the evolution of life on Earth. As we explore more tropical and subtropical caves, we can expect to be further amazed and challenged by the creativity and opportunism of evolution.

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