429. Romero, A. 2004. Evolution of hypogean fauna. pp. 347-349, *In*: J. Gunn, Ed.
Encyclopedia of Cave and Karst Science. New York: Fitzroy Dearborn.

EVOLUTION OF HYPOGEAN FAUNA

Hypogean fauna characterized by troglomorphisms have been used by virtually every school of thought in evolution in support of their theories, from 19th-century creationism to past and present neo-Lamarckism (including its derivatives of directional—"regressive"—evolution), and from the neutralist school to the selectionist / neo-Darwinian one. In fact, Darwin himself took a somewhat ambiguous position in the first edition of *On the Origin of the Species by Means of Natural Selection*, where he explained troglomorphism as a combination of both natural selection and use *vs.* disuse. In later editions he took a more neo-Lamarckian stance (for a review of these schools of thought, see Romero, 2001).

Evolution is opportunistic, and that is why life is ubiquitous on earth. The total number of troglomorphic species has been estimated to be between 50 000 and 100 000 (Culver & Holsinger, 1992). This number is considerable, given that most hypogean habitats: (1) are very reduced in space; (2) generally lack primary producers (plants); and, (3) have not been thoroughly explored, particularly in tropical regions where caves contain a very diverse fauna (Deharveng & Bedos, 2000).

Historically, most cave researchers have concentrated on hypogean animals that are troglomorphic. The hypogean fauna has thus been epitomized by animals displaying some kind of troglomorphism (see Table); however, not all hypogean faunas are troglomorphic. Surveys of cave fauna yield a large proportion of non-troglomorphic organisms; further, the proportion of troglomorphic organisms in caves is inversely proportional to latitude (Peck, 1988). The number of known hypogean fish species with troglomorphism is 86 (Romero & Paulson, 2001a) and 115 without troglomorphism (Poly, 2001). These data are consistent with the contention that a large proportion, perhaps even the majority, of hypogean animals worldwide are not troglomorphic. Therefore, colonization of the hypogean environment does not necessarily require morphological changes.

Some argue that hypogean environments are so "harsh" (i.e. poor in nutrients) that only "pre-adapted" organisms could survive in them (Holsinger, 2000). Available data do not support either generalization about the ecological conditions in caves or about the nature of the colonizing animals. First, animals that colonize caves can find food, reproductive niches, protection from predators, and a place for hibernation. Therefore, the hypogean environment can offer a number of ecological opportunities to many different species of many different taxa. That is why cave colonizers can undergo extensive adaptive radiations (leading to many differentiated populations and / or species) (e.g. Hoch & Howarth, 1999). Second, contrary to generalizations based on

Evolution of Hypogean Fauna: List of some features catalogued as "troglomorphic". (Not all troglomorphic organisms display all these characteristics at the same time.)

Morphological	Physiological	Behavioural
	Reduced or lost	
Eyes, ocelli	Metabolism	Photoresponses
Visual brain centres	Circadian rhythms	Aggregation
Pigmentation	Fecundity	Response to alarm substances
Pineal organ	Egg volume	Aggression
Body size		
Cuticles (terrestrial arthropods)		
Scales (fish)		
Swim bladder (fish)		
	Enlarged or increased	
Chemo- and mechanosensors	Lifespan	
Appendages	Lipid storage	

studies of caves in temperate regions (e.g. Poulson & White, 1969), many caves are very rich in nutrients, particularly in tropical regions (e.g. Deharveng & Bedos, 2000), and some are even chemo-autotrophic, that is, rich in bacteria that produce organic matter by oxidizing sulfur (see Movile Cave, Romania). Both types of caves tend to be very rich in species, and some of those species have large populations.

"Pre-adaptations" have been described as features such as nocturnal habits and hyperdevelopment of sensory organs in epigean species that are considered useful and even necessary in hypogean environments (Holsinger, 2000; Langecker, 2000). However, a recent study of hypogean fishes failed to show that all or even most fish families with troglomorphic representatives were taxa characterized by pre-adaptive features (Romero & Paulson, 2001b). Furthermore, the Texas blindcat *Trogloglanis pattersoni*, found in deep aquifers, has rather minute barbels, which is unusual for other catfishes of its family (Ictaluridae) (Langecker & Longley, 1993). This is inconsistent with the notion that enlarged sensory organs are required to enhance survival potential in the hypogean environment. Therefore, "pre-adaptations" are neither necessary nor sufficient to that end.

Caves around the world have very variable conditions, with a wide range of temperature, water supply, and size. The only thing they have in common is that for most of their length no natural light is available. The two characteristics most closely correlated with light conditions are eyes and pigmentation. Animals that have been raised under conditions of total darkness display a lower degree of eye and pigment development (see Adaptation: Eyes); conversely, when troglomorphic animals are exposed during certain periods of time to light, they may redevelop, to a certain extent, both pigmentation and the visual apparatus.

This strongly suggests that many troglomorphic animals are derived from epigean species characterized by phenotypic plasticity. Phenotypic plasticity is the ability of a single genotype to produce more than one alternative form of phenotype in response to environmental conditions. The direction and degree of response to environmental factors is known as the reaction norm, which is genetically variable and subject to natural selection. Natural selection may favour those individuals with a higher capacity to express specific traits under appropriate conditions. Phenotypic plasticity often provides a reproductive advantage over a genetically fixed one because environmentally induced phenotypes have a higher probability of conforming to prevailing environmental conditions than genetically fixed ones.

Lack of light can trigger heterochrony, i.e. changes in the timing of development of features. Examples are paedomorphs (animals that do not reach morphological maturity [metamorphs] reproducing as juveniles), and neotenes (animals with an unusually slow rate of growth). Many cave organisms are either paedomorphic or neotenic. Most troglobitic salamanders are paedomorphic, and half of all known paedomorphic salamanders are troglobites. Salamander evolution into a paedomorphic condition can be quite fast. Individuals living in the hypogean environment gain an advantage by becoming paedomorphic because this condition gives them the flexibility to survive in an unpredictable environment. Paedomorphosis in *Eurycea neotenes* seems to be a response to selection for the ability to pass dry periods in hypogean aquatic refugia (Sweet, 1977; see also Amphibia). Also, neoteny in hypogean animals is well documented for reduced body size, loss of scales, fin modifications, and reduced ossification.

Natural selection that favours paedomorphs / neotenes fixes their paedomorphic / 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. In fact, paedomorphosis can be achieved via a major gene effect (a small genetic change generating a large phenotypic effect). Troglomorphic characteristics can arise via minor changes in developmental genes.

Only when there is a constant gene flow from the epigean environment can such changes be prevented. In this respect the recessive allele can be considered the "troglomorphic gene" because it manifests a morphologically and ecologically differentiated phenotype that is reproductively isolated from the epigean ancestor. This explanation is supported by the convergent nature of troglomorphic characteristics. Convergent evolutionary patterns are strong evidence of adaptation via natural selection. Isolation would later lead towards speciation (genetic differentiation from the epigean ancestor; see Speciation). Many troglomorphic organisms are believed to have recently invaded the hypogean environment, since their epigean ancestor is easily recognizable and can even interbreed with them to produce fertile hybrids.

The evolution of troglomorphic characteristics does not necessarily occur in parallel. This is because: (1) they are controlled by sets of genes independent of each other; (2) the degree of development of these characteristics is conditioned by their phylogenetic history; and (3) because the selective pressures behind each one of those characteristics may differ from cave to cave (Culver *et al.*, 1995; Romero & Paulson, 2001c). In addition to reduction / loss of phenotypic characteristics, many troglomorphic organisms exhibit enhancement of sensory systems (chemical and mechanical) that are favoured by natural selection, since these sensory systems increase the fitness (survival capabilities) by helping them to find food and mates. Complex, coordinated, and adaptive phenotypes can originate rapidly and with little genetic change, via correlated shifts in the expression of plastic traits. Composite charactersistics, like those often observed among troglomorphic organisms, are produced by correlated phenotypic shifts that give the impression of a coevolved character set.

There are still grey areas in our understanding of the evolution of hypogean fauna. For example, we assume that behaviour plays a major role in the colonization of new niches, since behaviour is the most plastic part of the phenotype. Although changes in behaviour are well documented and present even in transitional forms, we do not know the role played by behaviour in the changes in other phenotypic characters. Behavioural changes usually precede external morphological evolution. Behavioural flexibility is thus the first condition for success in cave colonization. Only after colonization has taken place do morphological and physiological changes take place. Individual adaptability is the main target of selection. Behavioural invasion of a new environment by adults exposes the reaction norm of their progeny. Since hormonal production is closely linked to behaviour and hormones play a role in many developmental processes, there is a great potential for hormones to produce (or act as) developmental constraints. Therefore, the arrest in development of features could be due to diminishing hormonal production as a physiological consequence of the adaptation to the hypogean environment (i.e. many behaviours are no longer performed under conditions of darkness). This, in turn, could lead to the differential regulation of developmental genes.

The phenomenon of loss or reduction of phenotypic characteristics is not unique to troglomorphic organisms, and can be found among other animals such as parasites, deep-sea creatures, and the inhabitants of highly turbid waters. Also, limblessness and flightlessness are common among faunas living on small islands and high mountains. The loss of limbs among cetaceans is an example of a major evolutionary novelty by default. Even humans show loss or reduction of a number of characteristics inherited from their ancestors (Diamond & Stermer, 1999). Thus, troglomorphisms can be explained using well-known evolutionary mechanisms, without needing to resort to neo-Lamarckian explanations or terminology such as "regressive evolution". The study of this phenomenon has been largely neglected in mainstream evolutionary biology due to the sense that evolutionary novelties mean addition, not subtraction, of characteristics, and because of the way in which this biological phenomenon has been used by neo-Lamarckians to advance their own cause of either inheritance of acquired characteristics or the notion that evolution has some sort of directionality (Romero, 2001).

Aldemaro Romero

See also **Adaptation; Biodiversity in Hypogean Waters; Colonization; Speciation in Caves and Karst**

Works Cited

Culver, D.C. & Holsinger, J.R. 1992. How many species of troglobites are there? *National Speleological Society Bulletin*, 54: 79–80

Culver, D.C., Kane, T.C. & Fong, D.W. 1995. *Adaptation and Natural Selection in Caves: The Evolution of* Gammarus minus, Cambridge, Massachusetts: Harvard University Press

Deharveng, L. & Bedos, A. 2000. The cave fauna of southeast Asia. Origin, evolution and ecology. In *Subterranean Ecosystems*, edited by H. Wilkens, D.C. Culver & W.F. Humphries, Amsterdam and New York: Elsevier

Diamond, J. & Stermer, D. 1999. Evolving backward. *Discover*, 19: 64–68

Hoch, H. & Howarth, F.G. 1999. Multiple cave invasions by species of the planthopper genus *Oliarus* in Hawaii (Homoptera: Fulgoroidea: Cixiidae). *Zoological Journal of the Linnean Society*, 127: 453–75

Holsinger, J.R. 2000. Ecological derivation, colonization, and speciation. In *Subterranean Ecosystems*, edited by H. Wilkens, D.C. Culver & W.F. Humphries, Amsterdam and New York: Elsevier

Langecker, T.G. 2000. The effects of continuous darkness on cave ecology and cavernicolous evolution. In *Subterranean Ecosystems*, edited by H. Wilkens, D.C. Culver & W.F. Humphries, Amsterdam and New York: Elsevier

Langecker, T.G. & Longley, G. 1993. Morphological adaptations of the Texas blind catfishes *Trogloglanis pattersoni* and *Satan eurystomus* (Siluriformes: Ictaluridae) to their underground environment. *Copeia*, 1993: 976–86

Peck, S.B. 1988. A review of the cave fauna of Canada, and the composition and ecology of the invertebrate fauna of caves and mines in Ontario. *Canadian Journal of Zoology*, 66: 1197–1213

Poly, W.J. 2001. Nontroglobitic fishes in Bruffey-Hills Creek Cave, West Virginia, and other caves worldwide. *Environmental Biology of Fishes*, 62: 73–83

Poulson, T.L. & White, W.B. 1969. The cave environment. *Science*, 165: 971–81

Romero, A. 2001. Scientists prefer them blind: The history of hypogean fish research. *Environmental Biology of Fishes*, 62: 43–71

Romero, A. & Paulson, K.M. 2001a. It's a wonderful hypogean life: A guide to the troglomorphic fishes of the world. *Environmental Biology of Fishes*, 62: 13–41

Romero, A. & Paulson, K.M. 2001b. Scales not necessary: The evolution of scalelessness among troglomorphic fishes. *Program Book and Abstract, Joint Meeting of Ichthyologists and Herpetologists, 81st Annual Meeting of the American Society of Ichthyologists and Herpetologists, 2001* (abstract) (unpublished; available at http://www.asih.org/meetings/2001/abstracts_2001.htm)

Romero, A. & Paulson, K.M. 2001c. Unparalleled evolution: Blindness, depigmentation, and scalelessness do not run hand in hand among troglomorphic fishes. *2001 NSS Convention. A Cave Odyssey. July 23–27, 2001, Mount Vernon, Kentucky, Program Guide*, p.64 (abstract) (unpublished; available at http://www.macalester.edu/~envirost/abstract_unparalleled_nss.htm)

Sweet, S.S. 1977. Natural metamorphosis in *Eurycea neotenes*, and the generic allocation of the Texas *Eurycea* (Amphibia: Plethodontidae). *Herpetologica*, 33: 364–75