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SUBTERRANEAN ECOSYSTEMS

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Chapter 0

BACKGROUND AND GLOSSARY

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INTRODUCTION

As with other specialized subjects, a plethora of terminology and definitions has come to surround, sometimes to obscure, the discipline of biospeleology (speleobiology, stygobiology, ...), terms sometimes so subtly different – even synonymous – as to confound even researchers within the discipline (for a fuller treatment see, for instance, Camacho, 1992).

The terminology covers six main themes:

(1) How a species came to be underground.
(2) The degree of dependence of a species on the underground realm.
(3) Whether a species shows adaptations to the underground realm.
(4) Whether a species inhabits subterranean voids filled with water or with air, and which part(s) of each it inhabits.
(5) The delimitation of the various hypogean subsystems.
(6) The amount and origin of the energy source for the ecosystem.

As a background to this volume, the main themes recurring in biospeleology are introduced below, followed by a Glossary.

The subject of caves is well introduced by Gillieson (1997), while the literature pertaining to karst hydrology, encountered especially in the context of stygofauna, is accessible in Ford and Williams (1989).

How a species came to be underground

This issue is covered from different stances in several contributions to this volume (e.g. Chapter 21 by Holsinger, Chapter 22 by Humphreys, and Chapter 31 by Deharveng and Bedos) as the topic is all-pervasive within biospeleology, and the issue will not be pursued here at length.

Troglobites were long considered to be phylogenetic or distributional relicts driven into caves by climatic change, especially in the Pleistocene refugium model. Recently, cave colonization has been viewed as an active process – the invasion of a vacant habitat. Notwithstanding, the underground realm does harbour many distributional and phyletic relicts.

Anchialine waters (inland groundwater with current marine connections) harbour a distinct (Sket, 1996) and, in some areas, a predictable fauna (Yager and Humphreys, 1996).

Stygofauna with marine ancestry are considered to colonize the shore line and to become isolated inland by marine regression following a period of marine transgression (Stock, 1977; Boutin and Coineau, 1990; Notenboom, 1991; Holsinger, 1994).

The degree of dependence of a species on the underground realm

Organisms have many pathways of interaction with subterranean spaces (Gibert et al., 1994); some are only found underground, while others move in and out of the hypogean realm. More than twenty special nomenclature schemes have been proposed to describe these relationships, based on morphological, behavioural, and ecological adaptations of animals to underground life and on their presence or absence in caves (troglofauna; see review in Camacho, 1992).

In the Schiner–Racoviţă system (Schiner, 1854; Racovitza, 1907), cave-inhabiting animals are grouped by their degree of dependence on the cave environment: *troglobites* are species which do not exist outside caves; *troglophiles* may live and reproduce underground as well as in the epigean domain; while *trogloxenes* do not normally feed underground, but may enter caves actively (regular trogloxene) or passively (accidental trogloxene). Additional criteria have subsequently entered these purely ecological definitions, so that they have become a variable mix of biological and morphological criteria (Howarth, 1973: p. 142).

The lack of detailed ecological information for most cave-inhabiting species leads to ambiguity, and this is to some extent overcome by the concept of *troglomorphy* (Christiansen, 1962), which permits classification of the cave inhabitants using a less ambiguous morphological definition (troglomorphic/non-troglomorphic species) rather than the ecological one (troglobitic/troglophilic/trogloxenic species); but this term is itself being infiltrated by behavioural and physiological attributes (Table 0.1).

Table 0.1
Characteristics of cave organisms relative to surface organisms – troglomorphies [1]

Morphological
Specialization of sensory organs (chemo-, hygro- thermo- and baro-receptors)
Elongation of appendages
Reduction of eyes, pigments and wings
Cuticle thinning (in terrestrial arthropods)
Foot modification (in Collembola and planthoppers)
Scale reduction (in fish)
Ecological and behavioural
Slowing metabolisms
Starvation resistance
Relaxation and degeneration of circadian rhythms
Lowered fecundity
Increased egg volume
Increased life span
Behavioural
Decreased aggregation (in Collembola)
Reduced reaction to alarm substances (in fish)
Increased sensitivity to vibration
Reduced intraspecific aggression

[1] From Culver et al. (1995), after Christiansen (1992).

Many species found living underground display certain characteristic traits that are thought to be adaptive to underground life. These include both the reduction or loss of characters (regressive evolution) and the enhancement of others (constructive evolution), which together produce the convergence, characteristic of cave-adapted animals, that is termed troglomorphy. These adaptations include morphological, ecological, physiological and behavioural characteristics (Table 0.1).

Whether a species shows adaptations to the underground realm

Organisms have many pathways of interaction with the subterranean realm. While some are only found underground, others move in and out of the hypogean environment as indicated in the ecological classification of species by the terms troglo(stygo)bitic, troglophilic and trogloxenic.

It is important to note that functionally these categories are more diffuse than is suggested by their ecological context. For example, while stygo(troglo)-xenes may occur underground only accidentally, they may influence happenings in the hypogean realm, for example, functioning either as predators or prey (e.g. Gibert et al. 1994: p. 11), as well as constituting a subset of the allochthonous inputs from epigean sources.

In considering troglomorphic correlates (e.g. reduced eyes, pigment, wings etc.) it is necessary to distinguish whether the traits are different from close epigean ancestors (*apomorphic*) or simply characteristics of the group or lineage (*plesiomorphic*).

Whether a species inhabits subterranean voids filled with water or with air, and which part(s) of each it inhabits

While the Schiner–Racoviţă system is often used for both terrestrial and aquatic species, Gibert et al. (1994: p. 13) have proposed stygo- (*sensu lato*) as the most ecologically descriptive prefix for groundwater fauna. Hence, *troglofauna* becomes restricted to terrestrial systems (see review in Camacho, 1992), while the aquatic fauna is referred to generally as *stygofauna* (Ginet and Decou, 1977; Botosaneanu, 1986; Gibert et al., 1994). There are complex parallel classifications in use for aquatic subterranean organisms (e.g. Botosaneanu, 1986: endpaper; Williams, 1984; Stanford and Ward, 1993).

Gibert et al. (1994) followed the main Schiner–Racoviţă system, replacing the prefix "troglo-" by "stygo-" (hence, stygoxene, stygophile, stygobite). In porous aquifers, stygophiles are subdivided into three categories: *occasional hyporheos,* which comprises essentially the larvae, especially of aquatic insects, of most of the benthos; *amphibites,* whose life cycle requires the use of both surface and groundwater systems; and *permanent hyporheos,* which comprises a diverse assemblage of organisms present in all life stages in the groundwater or in the benthic habitats – an aerial epigean stage is not required to complete the life cycle.

Stygobites are subdivided into two classes of obligatory hypogean forms: *ubiquitous stygobites* are widely present in both karstic and alluvial groundwaters and are sometimes found very close to the surface. In contrast, *phreatobite* species are stygobites that are restricted to the deep groundwater substrata of alluvial aquifers (Gibert et al., 1994).

Delimitation of the various hypogean sub-systems

The hypogean realm used to be defined in terms of caves and the degree of darkness. The realization that most caves had no openings to the surface (Curl, 1966), and that troglobitic animals may inhabit the immediate subsurface spaces even in non-karstic areas (Uéno, 1977; Juberthie et al., 1980; Juberthie and Delay, 1981), means that the limits to the hypogean realm are difficult to define. At the surface, epigean and edaphic environments may grade imperceptibly into the hypogean realm, while at the lower end of the hypogean realm the metazoans progressively fade away, leaving a microbiological world that may penetrate deep into the Earth's crust (Gold, 1992).

This complexity is apparent also at a finer scale. For example, the hyporheic zone is an ecotone between surface water and groundwater, but this ecotone is difficult to define. It has been variously interpreted in both physical and biological terms: physically by the depth to which the river water penetrates into the hyporheic zone, and biologically by the depth to which amphibites penetrate into it. In reality, it is a region of great complexity, the origin of the water being from either groundwater (upwelling zone) or surface water (downwelling zone). It is best considered as a dynamic ecotone or transition zone (see Gibert et al., 1994).

In large caves the highly troglomorphic species are generally considered to be restricted to the deep cave environments where the temperature is stable and the air is saturated with water vapour, and frequently contains elevated levels of carbon dioxide. Nonetheless, in some tropical areas (Cape Range, Australia), highly troglomorphic (and stygomorphic) species are found, under certain conditions, to be feeding in sunlight at the entrance to caves. However, even within caves, the boundaries between zones are dynamic, shifting, *inter alia,* according to the degree of biogenic carbon dioxide production (dependent on periodicity of water and energy inputs), the weather, the season and major climatic events. The extent of the zones and their vagility varies between caves according to the relative sizes of entrances and volume, and the size, shape and arrangement of the chambers (see Racovita, Chapter 28, this volume).

The amount and origin of the energy source for the ecosystem

In the absence of light subterranean ecosystems have been considered to be dependent on organic matter fixed by photosynthesis and reaching the hypogean realms by various direct and indirect pathways. Routes of entry are as diverse as logs being washed into open caves, dissolved organic matter percolating downwards through a porous medium into caves otherwise closed to the surface, and animals such as bats and crickets moving between the cave and the exterior.

Diverse subterranean ecosystems dependent upon the chemoautotrophic bacteria that rely on sulphides have recently been demonstrated (see Chapter 17 by Sarbu, Chapter 18 by Pohlman et al., and Chapter 19 by Sarbu et al.). Sulphides may be of magmatic or petroleum origin (see Chapter 12 by Poulson and Lavoie) and these caves are thus analogous to the deep-sea environments of hydrothermal vents (Childress and Fisher, 1992) and cold seeps (Arp and Fisher, 1995; Scott and Fisher, 1995), respectively.

Underground environments are typically considered to be sparsely provided with food energy – to have a low energy density – and it is hypothesized that this is a major selective pressure involved in the loss of characters, such as eyes, in troglobites. This low energy density may be evenly distributed and so difficult to harvest, or it may occur as sparsely distributed bundles of high energy and thus be difficult to find. A few systems have profuse and predictable supplies of energy usually transported into the system by animals (bats, birds and crickets) or flowing water (some chemoautotrophic systems).

TERMINOLOGY

As indicated above, biospeleology has developed a range of special terms to cover its subject matter. In addition, the terminology of speleology is frequently encountered in biospeleological literature. This vocabulary is covered well in Lowe and Waltham (1995), and the equivalent terms in English, German, French and Hungarian are listed by Attila (1996).

Specialized terms are listed and explained in the Glossary below, together with a range of terms in related disciplines which may be unfamiliar to the reader. Additional terms can be found in Lincoln et al. (1982).

GLOSSARY

Aesthetasc. Sensory or olfactory bristles on the antenna or antennules of many arthropods.

Allochthonous. Originating outside the habitat under discussion.

Allopatric. Used of species or populations occupying a geographical area different from that of another species or population.

Amensalism. An interspecific interaction in which one species population is inhibited, typically by toxin produced by the other, which is unaffected.

Amphibite. Particular type of stygophile species whose life cycle requires the use of both surface water and groundwater systems; also *amphibionts.*

Anchialine (or anchihaline). Anchialine habitats consist of bodies of haline waters, usually with a restricted exposure to open air, always with more or less extensive subterranean connections to the sea, and showing noticeable marine as well as terrestrial influences (Stock et al., 1986). They typically occur in volcanic or limestone bedrock (Iliffe, Chapter 3, this volume).

Apomorphic. Pertaining to a derived character within the taxa being considered, in contrast to the ancestral (plesiomorphic) state.

Aquiclude. Body of relatively impermeable rock or sediment acting as a boundary to an aquifer.

Autapomorphy. The possession of a unique derived character by a species or monophyletic taxon; *cf.* Synapomorphy *q.v.*

Aven. Hole in a cave roof, which may be a blind pocket or a tributary inlet shaft, and known as dome-pits in the United States; locally in France the term for pothole.

Biofilm. Accumulation of bacteria attached to solid surfaces by means of appendages and exopolymers, in which condition cross-feeding is favoured and they are protected from dislodgment, predation and adverse physico-chemical conditions (Gounot, 1994).

Blue hole. (1) Non-turbulent resurgence (Jamaica); (2) drowned sinkholes on the Bahamas Banks from which cooler water rises during high tide (Bahamas); (3) generally, shaft-like depressions deeply flooded by sea water, typically in low-lying coral islands.

Boundstone. Carbonate rock whose components were bound together during deposition and remain in position of growth, such as many reef rocks.

Calcarenite. Wackstones, *q.v.* (Gary, McAfee and Wolf, 1972).

Calcrete. Carbonate deposits that form in the soil or in the vicinity of the groundwater table as a result of the evaporation of soilwater or groundwater respectively. Groundwater calcretes form in arid climates (annual rainfall less than 200 mm) with high potential evaporation (more than 3000 mm per year: Mann and Horwitz, 1979).

Cave (*sensu lato*). Underground void, generally of a size sufficient for people to enter. However, the word means different things to different people. Cavers treat as caves natural holes large enough to enter – sometimes the term pothole is applied to vertical developments – or which extend to darkness. Archaeologists often use the term loosely to include rock-shelters. In geomorphological terms, a cave is an opening of diameter or width greater than 5–15 mm – that is, a void of sufficient dimensions to allow turbulent rather than laminar flow of water (Ford and Williams, 1989). These differences are well reconciled by Howarth (1983: p. 370) “In both soluble and volcanic rocks, therefore, a complex of interconnected voids of varying sizes anastomoses throughout the rock in a great labyrinthine system. Within this system there is a continuum of various sized voids from the microscopic to the largest caverns. The existence of these voids, their size, depth, and extent, depends on the geological history of the area. From a biological perspective, this continuum can be divided into three size classes: microcavernous (<0.1 cm), mesocavernous (0.1–20 cm) and macrocavernous (>20 cm)”.

Cave lint. The accumulation on cave formations of detritus (skin, fibres, hair, etc.) shed by human visitors to caves; mainly a problem in busy tourist caves.

Cavernicole. Pertaining to an inhabitant of caves *sensu lato,* without implying any particular dependence on, or association with the cave environment.

Cenote. Flooded collapse depressions on flat limestone plain – originally from Yucatán, Mexico.

Chaetotaxic. Pertaining to the arrangement or pattern of bristles.

Chemoautotrophs. Organisms deriving nourishment from chemical reactions of inorganic substances, as in sulphur and iron bacteria.

Chemoheterotrophs. Organisms that obtain energy from oxidation/reduction reactions and use organic electron donors; cf. chemoorganotrophs.

Chemolithoautotrophs. Organisms that obtain energy from oxidation/reduction reactions and use inorganic electron donors.

Chemotrophs. = Chemoautotrophs.

Cleitric. The fissure system in the rock matrix in contradistinction to the cave (speleic) system.

Cockpit karst. Synonym of Cone karst, referring to the depressions.

Compartiment souterrain superficiel. = Superficial underground compartment, *q.v.*

Cone karst. Karst type of tropical regions characterized by an extent of steep, conical hills and adjacent star-shaped depressions, or cockpits having steep, convex sides and slightly concave floors.

CPOM. Coarse particulate organic matter [for example, dead leaves and twigs; *cf.* FPOM, *q.v.*].

Craton. Part of the Earth's crust little deformed for a prolonged period (shield region).

Crenobionts. Inhabitants of springs and spring brooks.

Crevicular. Pertaining to the finer cracks, crevices and spaces within rock matrix.

Cryptokarst. Karst secondarily covered by sediments.

Cyclothemic. In Jurassic limestone of central Italy, pertaining to a cyclic sedimentation controlled by climatic events (Cycle of Milankovitch: Milankovitch, 1920).

Dark zone. Region of cave in perpetual total darkness.

Decoration. Speleothems, *q.v.*

Decomposer. Any organism that feeds by degrading organic matter.

Deep (zone) cave environment. Region of cave with constant temperature and near-saturated humidity; the most troglomorphic species are often restricted to this region.

Distrophic. Pertaining to caves mostly supplied with vegetal matter during floods.

Doline. Simple closed circular depression in karst area with subterranean drainage and commonly funnel-shaped, varying from a few to many metres in dimensions.

DOM. Dissolved organic matter, typically $<1\ \mathrm{mg}\,\ell^{-1}$ in pristine groundwater.

Dripstone. = Flowstone, *q.v.*

Dysaerobic. Environments in which the oxygen concentration is between 0.1 and $1.0\,\mathrm{ml}\,\ell^{-1}$.

Edaphobite. Deep soil inhabitant.

Edaphon. The biota living within the soil or substrate – *cf.* Psephon, Edaphobite, *q.v.*

Embryonic genesis (embryogenesis). Embryonic development from an ovum.

Endobenthos. Organisms living within the substratum, as, for example, burrowing species.

Endogenous zone. The zone immediately beneath the Earth's surface.

Endopsammic. Pertaining to inhabitants of water-saturated sand.

Entrance zone of cave. Area of cave where outside influences dominate both the physical and biological environment.

Epibenthic. Living on the surface of the sea bed or lake floor.

Epigean. The surface environment as opposed to the subsurface (subterranean, hypogean) environment.

Epikarst. Upper part of the percolation zone.

Epiphreatic. Inhabiting the superficial part of the Phreatic zone, *q.v*; the vadose–phreatic boundary.

Euryece. Inhabiting a wide range of habitats.

Eurytopic. Having a wide geographical distribution.

Eutrophic. Pertaining to a large amount of available organic matter, high energy density or nutrient enrichment; in caves especially that provided by bat guano or flood debris.

Exaptation. Adaptation for one function serving for another function.

Exokarst. All features that may be found on the surface of a karst landscape, ranging in size from tiny *karren* to massive *poljes.*

Exploitative competition. An interaction between organisms in which one benefits at the expense of the other.

Flowstone. Deposit formed from trickles or films of water on walls and floors of caves, normally of calcite.

Fluviokarst. A karst landscape where the dominant landforms are valleys cut by surface rivers – the valleys become dry as karst development improves underground drainage.

Fossil cave. Cave no longer containing a stream or active speleothems.

Foul-air zone. Still-air zone of a cave, usually in a depression or pot, with high humidity and elevated carbon dioxide levels, which may result from biogenic or physical effects (see, for instance, Howarth and Stone, 1990).

FPOM. Fine particulate organic matter resulting from abrasion and mechanical disruption by biological and physical agents; *cf.* CPOM.

Gelifraction. Mechanical disintegration of rock or soil caused by the freezing of contained water (also congelifraction).

Ghyben–Herzberg principle. Expression of the relationship which occurs in near-coastal porous aquifers where fresh water overlies sea water; the depth below sea level of the fresh water/salt water interface is ~40 times the height of the water table above sea level; thus a minor drawdown of the groundwater can lead to a major intrusion of sea water into an aquifer by upward coning of the salt water in response to a thinner freshwater layer. Hence, Ghyben–Herzberg system or lens. (See Chow, 1964.).

Grainstones. Mud-free carbonate sedimentary rock.

Grieta. Crevice, fissure, crack or cleft in Spanish.

Guanobite. Species that, when in caves, inhabit guano deposits (from bats, swiftlets, etc.), and whose entire life cycle takes place in this substrate (see Gnaspini and Trajano, Chapter 13, this volume).

Guanophages. Species that feed directly on guano, or on microorganisms and fungi that grow on it (see Gnaspini and Trajano, Chapter 13, this volume).

Guanophile. Species that may inhabit and reproduce both in guano piles and in other substrates in the cave environment (see Gnaspini and Trajano, Chapter 13, this volume).

Guanoxene. A species feeding and/or reproducing in guano deposits but depending on other substrates in the cave to complete its life cycle (see Gnaspini and Trajano, Chapter 13, this volume).

Haematophagy. Feeding on blood.

Halocline. More or less abrupt change in salinity with depth in water column.

Heterochrony. Change in timing or rate of developmental events, relative to the same event in the ancestor.

Hom[o]eotic mutation. Mutation from one state to another of a structure that exist in a series of states, such as the mutation of an insect wing into a haltere.

Homoplasy. Structural resemblance due to parallelism or convergent evolution rather than to common ancestry.

Hypogean. The subsurface or subterranean environment as opposed to the surface (epigean) environment.

Hyporheos [hyporheic zone]. Interstitial spaces within the sediments of a stream bed; a transition zone between surface water and groundwater (Orghidan, 1959).

Impounded karst. Karst system in which the underground drainage is dammed, typically by another lithology, sometimes resulting in dammed springs.

Interstitial. Living in the spaces between particles, especially in alluvia.

Iridophore. Colour cells containing guanine in, for example, fishes, reptiles, spiders and butterflies; iridocytes.

Isopiestic. Regions of an aquifer where the pressure head of ground water is the same.

Karren. Synonym of Lapiaz.

Karst. Soluble-rock landscape; terrain with distinctive hydrology and landforms arising from a combination of high rock solubility and well-developed secondary porosity. The distinctive landforms above and below ground that are the hallmark of karst result from the solution of rock (mainly by carbonic acid) along pathways provided by the structure. The unusual features of the Kras (Karst in the period of the Austro–Hungarian empire) region on the Italo–Slovenian border became known as "karst phenomena". Such areas are characterized by sinking streams, caves, enclosed depressions, fluted rock outcrops and large springs (Ford and Williams, 1989).

Karstification. Production of karstic features on the landscape.

Karst window. A section of groundwater exposed by roof collapse or dissolution, especially in karstlands, as, for example, an anchialine pool.

Kipuka. Isolated protrusion of bedrock (in Hawaii) in lava flow, such as the summit of a hill; synonym: steptoe.

Lapiaz. In karst terrain, a general term for solutional furrows in a limestone surface, with depths between a few millimetres and more than a metre, usually separated by knifelike ridges; synonym of karren. (Pyrénées dialect, also *lapiés*.).

Lava tubes. Tubular caves within lava flows, subject to mechanical collapse of the roof (vulcanokarst).

Lavicole. Pertaining to an inhabitant of lava beds.

Lentic. Standing water as in swamp, lake, pond.

Limnicoid. Inhabiting lakes; also, limnicole.

Limno- (Prefix). Restricted to fresh water.

Limnostygobionts. Stygobionts restricted to fresh waters.

Lotic. Running water, as in stream or river.

Lucifuge. Intolerant of light.

Macrocavernous. Underground voids >20 cm, especially caves and underground passages in karst and volcanic substrates.

Mafic. Said of igneous rock composed of one or more ferromagnesian minerals.

Manna. Honeydew secreted by some scale insects (Coccidae).

MAST (or M.A.S.T.). The mean annual surface temperature of a region – the expected temperature of the deep cave environment in the absence of significant geothermal heat or internal climatic effects.

Meiobenthic. Small benthic (*q.v.*) organisms that pass through a 500 µm sieve but are retained by a 40 µm sieve; *cf.* meiofauna, *q.v.*

Meiofauna. Assemblage of animals that pass through a 500 µm sieve but are retained by a 40 µm sieve, often interstitial; prefix meio-, hence meiobenthic.

Mesocaverns. Underground voids in the size range 0.1–20 cm, especially in karst and volcanic substrates.

Mesopsammon. Psammon *q.v.*

Mesovoid shallow stratum. See superficial underground compartment.

Mesotrophic. Pertaining to an intermediate amount of available organic matter, medium energy density.

Messinian. Part of Miocene epoch ~6.5–5.5 million years ago. The Mediterranean area was landlocked and almost completely dried out at this time, leaving a series of hypersaline lakes which had profound implications for the aquatic fauna, hence the Messinian Salinity Crisis.

Microvoid. See mesocaverns.

Milieu souterrain superficiel. = Superficial underground compartment.

Mixohaline. Water with a salinity between 5 and 30‰ under the Venice System (equivalent to 5000 and 30 000 mg ℓ^{-1} total dissolved solids).

Mixture corrosion. The ability of two calcite-saturated water masses of different carbon dioxide content to dissolve additional calcite when mixed.

MSS. = Superficial underground compartment.

Nappes phreatiques. Pertaining to sheet flow in deep groundwater.

Nectarivory. Feeding on nectar.

Neogeoaeolian. Pertaining to an ecosystem within a newly formed landscape (lava flows, sand cays) supported by windborne allochthonous material (Howarth, 1979).

Neoteny. Paedomorphosis (*q.v.*) produced by retardation of somatic development, so that sexual maturity is attained in an organism retaining juvenile characters; *cf.* Progenesis.

Neuromast. Sensory receptor, part of the acousticolateralis system of aquatic chordates, to detect vibration and movement in water.

Neutral mutation. A genetic mutation that proffers no advantage or disadvantage to the organism.

Nomocoenosis. Pasture community.

Normoxic. Pertaining to habitats with the normal level of oxygen found in the atmosphere or dissolved in water in equilibrium with it.

Nycthemeral. Occurring at night.

Oligotrophic. Pertaining to low amount of available organic matter, low energy density.

Outgroup. A distinct but closely related species or lineage used as an anchor in phylogenetic and cladistic analyses.

Packstones. Sedimentary carbonate rock whose granular material is self-supporting yet contains calcareous mud.

Paedogenesis. Paedomorphosis (*q.v*) produced by precocious sexual maturity in an organism that is still at a morphologically juvenile stage; *cf*. Neoteny, Progenesis *q.v.*

Paedomorphosis. Retention of sub-adult ancestral traits in the descendant adult.

Palaeokarst. A rock or area that has been karstified and subsequently covered by sediments.

Paludicole. Pertaining to an inhabitant of marshes.

Parafluvial. Pertaining to groundwater adjacent to the river channel.

Parapatric. Pertaining to populations whose geographic ranges are contiguous but not overlapping, so that gene flow between them is possible.

Peripatric. Peripheral to the main distribution, as used in 'speciation in peripatric populations'.

Philopatric. In the context of bats, loyalty to caves (maternity or hibernal) or other roosts (Tuttle, 1976). It is applied to bats which return to the same caves on a daily and/or on a seasonal basis; thus, the bat colonies tend to be stable.

Photoautotroph. Organisms that obtain metabolic energy from light by a photochemical process; = Phototroph, *q.v.*

Photoheterotroph. Organism that utilizes radiant energy and organic electron donors (synonym: photoorganotroph).

Photo-negativity. The avoidance of light.

Phototroph. = photoautotroph, *q.v.*

Phreatic. That part of a cave system lying below the local groundwater table; below the unsaturated or vadose zone, *q.v.*

Phreatic loop. Water-filled cave tube rejoining itself.

Phreatobiological net. Net designed to sample deep groundwater, usually through bores and wells.

Phreatobite. Stygobites that are restricted to the deep groundwater substrata of alluvial aquifer (phreatic water) (Gibert et al., 1994).

Phreatomorphic. Pertaining to the convergent morphological, behavioural and physiological features of phreatobites – Stygomorphy, Troglomorphy, *q.v.*

Phreatos. Assemblage of organisms inhabiting deep groundwater (phreatic zone).

Phytophilic. Plant-eating = phytophagous, herbivorous.

Pleiotropic. Pertaining to a gene that has more than one phenotypic effect.

Pleistocene refugium model. Traditional model for isolation of species in caves including both dispersalist and vicariant elements. Ancestral populations are isolated in caves by climatic change without active invasion. The genetic bottleneck resulting from small founder population is followed by reorganization of epigenotype. Subsequent subterranean dispersal expands the geographic range as adaptation improves.

Plesiomorphic. Pertaining to an ancestral character within the taxa being considered, in contrast to the derived (apomorphic) state.

Poecilotrophic. Pertaining to variable amounts of organic matter, as in long caves with sections differing in energy density, ranging from oligotrophic to eutrophic.

Polje. Large closed depression – with a flat floor that makes a sharp break with surrounding slopes – draining underground, often containing a stream and liable to flood, becoming a lake.

Pre-adaptation. Possession by an organism of the necessary properties to permit a shift into a new niche or habitat. A structure is preadapted if it can assume a new function before it becomes modified itself.

Progenesis. Early cessation of developmental events in the descendant; produces paedomorphic traits when expressed in the adult phenotype; early sexual maturation will produce global progenesis, but early cessation in local growth fields can also produce progenesis (McNamara, 1990).

Provincialization. Progressive formation of morphologically or genetically distinct subpopulations in a region having previously a more homogeneous population.

Psammolittoral. Pertaining to sands along lake and sea shores.

Psammon. Organisms living between sand grains of freshwater or marine shores; Mesopsammon.

Psephon. Interstitial water dwellers (equivalent to Edaphon; unusual).

Pseudokarst. Karst-like landforms produced by processes other than solution or corrosion-induced subsidence and collapse; e.g. ice caves (Ford and Williams, 1989).

Pycnocline. More or less abrupt change in water density with depth, typically at the halocline or thermocline in the water column.

Regressive evolution. The loss of morphological and behavioural characters that accompanies isolation in caves.

Refuge (refugium, refugia). A region in which certain types or suites of organisms are able to persist during a period in which most of their original geographic range becomes uninhabitable because of climatic change (Morton et al., 1995).

Syntopically. Pertaining to populations or species that occupy the same microhabitat, are observable in close proximity, and could thus interbreed.

Tabular karst. Broad expanse of more or less horizontal karst.

Thalasso-. (Prefix) Pertaining to marine or brackish waters, hence thalassostygobionts, thalassopsammon and thalassopsephon.

Thalassoid. Having marine affinities.

Thermocline. More or less abrupt change in temperature with depth in air or water column.

Thigmotactism. The tendency of many small organisms to seek maximum surface contact, as in corners and crevices.

Tower karst. Residual karst hills with near-vertical to overhanging lower slopes, often separated by areas of alluvial deposits.

Transition zone of cave. A dynamic zone in total darkness where the microclimate is still conspicuously affected by short-term meteorological events at the surface.

Troglo-. (Prefix) For subterranean terrestrial and aquatic systems, now more commonly restricted to terrestrial systems, being replaced by "stygo-" for aquatic systems.

Troglobiont. Animal inhabiting the various types of subterranean spaces; sometimes restricted to air-filled voids; and hence terrestrial as opposed to aquatic species.

Troglobiontic stygobionts. Obligate inhabitants of underground waters found in caves.

Troglobite. Species which do not exist outside caves (Schiner, 1854); they may, however, occur in the superficial underground compartment or in the upper hypogean zone.

Troglobitization. = Troglogenesis.

Troglogenesis. The morphological, behavioural, physiological and other changes found in species/lineages as they populate/adapt to cave or hypogean life.

Troglomorphic. Pertaining to morphological, behavioural and physiological characters that are convergent in subterranean populations (Christiansen, 1962).

Troglophile. Species able to live and reproduce underground as well as in the epigean domain.

Troglos. Assemblage of organisms inhabiting underground voids, often restricted to the 'terrestrial' organisms in air-filled voids.

Trogloxene. Species that do not normally feed underground, but may enter caves actively (regular trogloxene) or passively (accidental trogloxene) (Racovitza, 1907).

Tropical winter effect. The drying of the air in tropical caves in winter when the cave temperature and the partial pressure of water vapour inside the cave exceed those outside the cave, resulting in the loss of water from the cave air (Howarth, 1980).

***Trou* technique.** Sampling method for fauna sediments involving filtering the water that has percolated into a hole dug in stream bank; synonym: Karaman–Chappuis method.

Twilight zone of cave. Region of cave extending from the limit of green vascular plants to total darkness; physical climate not stable.

Upper hypogean zone. Region immediately above the bedrock where the high porosity provides suitable hypogean habitat for troglobites (Uéno, 1987); = Superficial underground compartment, *q.v.*

Vadose zone. The zone of rock above the water table, mostly free-draining; also called the unsaturated zone, and lying above the saturated or phreatic zone, *q.v.*

Vauclusian. A spring rising from a vertical or very steep flooded bedrock cave passage directly draining the phreatic zone and emerging in daylight; named after the type example, La Fontaine de Vaucluse in southern France.

Vicariance. Speciation as a result of range disruption, typically the result of some non-biological process; also termed passive allopatric speciation.

Vicariant event. The division of the biota or taxon through the development of a natural barrier.

Wackstones. Mud-supported carbonate sedimentary rocks containing >10% grains (particles >20 μm in diameter), e.g. calcarenite.

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